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ERRATA

Page 46, legend of Fig. 2. For 'B, bract (×½); C, sepal (×½); D, petal (×½); E, androecium and gynoecium (×1)' read 'C, bract (×½); D, sepal (×½); E, petal (×½); B, androecium and gynoecium (×1)'

Page 74, line 30. For 'the scales are about as long as the anthers' read 'the scales are about ½ as long as the anthers'

Page 179, line 17. For '*Commelina virginica* L.' read '*Commelina erecta* L.'

Page 187, line 9. For '*Odum 2273*' read '*Blum, Duke & Odum 2273*'

Page 200, lines 22 & 23. For '(as observed in Johnston 3426, DAV), although seeds of Panama plant differences.' read 'fruits of *B. macrophylla* are collected, these may prove to show additional differences.'

Page 363, line 18. For 'flower' read 'flowers'

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Annals
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Volume 54 1967 Number 1

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 95. VOCHYSIACEAE[1]

BY ANDRÉ ROBYNS[2, 3]

Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Trees or shrubs, infrequently herbs, often with resinous sap. *Leaves* opposite or verticillate, the stipules small and deciduous or absent, sometimes reduced to glands, the blade simple, entire-margined, penninerved. *Inflorescences* terminal and axillary, racemose, paniculate or thyrsoid, sometimes flowers axillary and solitary. *Flowers* ☿, obliquely zygomorphic, usually bibracteolate; calyx gamosepalous, the 5 lobes quincuncial, unequal or rarely subequal, one of the lateral lobes (the fourth one) usually much larger than the other ones and spurred or gibbous at the base; corolla usually perigynously inserted on the calyx, the petals free, rarely 5 and imbricate, usually 1 or 3, unequal and convolute, unguiculate, variously colored; androecium inserted with the corolla, reduced to 1 fertile stamen, the anther introrse, bithecate, longitudinally dehiscent; pollen 3-colporate; staminodes often present; gynoecium 3-carpellate, the ovary superior, 3-locular and with

[1] Assisted by National Science Foundation Grant No. GB-170 (Principal Investigator, H. C. Cutler).

[2] Visiting Curator of the Flora of Panama, Missouri Botanical Garden; *Chargé de Recherche* of the National Foundation for Scientific Research, Belgium.

[3] I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and for the loan of material: Field Museum of Natural History, Chicago, Illinois (F) and U. S. National Herbarium, Washington, D. C. (US).

ANN. MISSOURI BOT. GARD. **54**(1): 1-7, 1967.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **53**, No. 3, pp. 265-388, was published on December 30, 1966.

1-∞ ovules per cell, rarely ovary almost inferior and 1-locular with 1-2 ovules, the placentation axile, the ovules anatropous; style simple, the stigma 1. *Fruits* usually capsular and loculicidally 3-valvate or infrequently unilocular, indehiscent and enclosed by the accrescent calyx lobes (samaroid); seeds alate, the wing mostly unilateral and consisting of numerous long hairs inserted on the testa, exalbuminous; embryo straight; cotyledons mostly convolute.

A family of six genera, all but one, the tropical African genus *Erismadelphus* Mildbr., distributed in tropical America; two presently reported from Panama.

a. Petals 3; stamen alternating with the third and fifth sepals (i.e. opposite the anterior petal); locules of the ovary 2-ovulate ..... 1. *Vochysia*

aa. Petal 1; stamen opposite the fifth sepal; locules of the ovary several-ovulate, the ovules biseriate ..... 2. *Qualea*

1. VOCHYSIA

Vochysia Aubl. corr. Poir., Encycl. Méth. Bot. **8:** 681, 1808, nom. gen. conserv. *Vochy* Aubl., Hist. Pl. Gui. Fr. 18, 1775.

Trees, shrubs, infrequently herbs. *Leaves* opposite or verticillate, petiolate, the stipules small and deciduous; blade coriaceous, the midvein prominent on the lower surface. *Inflorescences* terminal and axillary, thyrsoid with helicoid cymes as partial inflorescences. *Flowers* with the calyx lobes unequal, one of the lateral lobes (the fourth one) much larger than the others and usually spurred at the base, the other lobes usually 1/4 as long as the spurred one or less; corolla yellow or orange-yellow, the petals usually 3, rarely 1 or none, the anterior or center petal alternating with the third and fifth sepals, and mostly larger than the others; stamen opposite the anterior petal; staminodes usually 2, opposite the lateral and posterior petals, small; ovary superior, 3-locular, the ovules 2 per locule. *Capsules* markedly 3-angular, 3-celled, the pericarp coriaceous or ligneous, the exocarp blackish, the endocarp golden-yellow; seed 1 per cell, the wing unilateral, the testa chartaceous.

A neotropical genus of about 100 species, monographed by Stafleu in 1948 (Rec. Trav. Bot. Néerl. **41:** 397-540); two species presently known from Panama.

a. Branchlets, lower surface of the leaf blades, and inflorescence axes ferruginous-tomentellous or ferruginous-puberulous; leaf blades acuminate to caudate-acuminate at the apex, the acumen up to 15 mm long; spur strongly arcuate, about as long as the blade; petals 9-10 mm long; capsule obtuse or subretuse at the apex, 1.7-2.5 cm long ..... 1. *V. ferruginea*

aa. Branchlets, lower surface of the leaf blades, and inflorescence axes glabrous or sparsely puberulous; leaf blades rounded or obtuse and usually ± retuse at the apex; spur straight or only slightly arcuate, ca ½-⅔ as long as the blade; petals ca 4-5 mm long; capsule acute to subacute at the apex, 3-4.5 cm long ..... 2. *V. hondurensis*

1. **Vochysia ferruginea** Mart. in Mart. & Zucc., Nov. Gen. Sp. Pl. **1:** 151, *t. 92,* 1824; Pittier, Contr. U. S. Nat. Herb. **18:** 237, 1917; Stafleu, Rec. Trav. Bot. Néerl. **41:** 494, 1948.—Fig. 1.

Cucullaria ferruginea (Mart.) Spreng. in L., Syst. Veg. ed. 16, **4,** Cur. Post.: 9, 1827.
Vochysia tomentosa Seem., Bot. Voy. Herald 120, 1852, non (G. F. W. Meyer) DC. (Prodr. **3:** 26, 1828).
Vochya ferruginea (Mart.) Standley, N. Amer. Fl. **25:** 302, 1924.

Tree 6-20 (35) m tall, the trunk straight, up to 60 (80) cm in diam, branchless for ca ½-⅔ of its length, the branches ascending and forming a spreading crown, the bark grayish and smooth, the branchlets softly ferruginous-tomentellous. *Leaves* opposite, the petiole canaliculate above, 5-8 mm long, softly ferruginous-tomentellous, the stipules 1-2 mm long; blade narrowly elliptic-oblong to narrowly elliptic, attenuate-cuneate at the base, acuminate to caudate-acuminate at the apex, the acumen up to 15 mm long and shortly mucronulate, the margins subrevolute, 5-12.5 (16) cm long and 2-4.5 (5) cm wide, the upper surface almost shining, glabrous and with the midvein impressed, the lower surface dull, ferruginous-puberulous, the indumentum especially dense along the prominent midvein and lateral veins. *Inflorescences* terminal and axillary, elongate-cylindrical, many-flowered, the cincinni 1-5-flowered, the rachis as the peduncles and pedicels softly ferruginous-tomentellous, the peduncles 2-4.5 mm long, the pedicels slender and up to 4-5 mm long. *Flowers* with the calyx reddish-orange, the spurred lobe fleshy, cucullate at the apex, 7-9 mm long (without spur) and ca 4 mm wide, sparsely and minutely puberulous at the base, the spur strongly arcuate, about as long as the lobe, sparsely and minutely puberulous, the other lobes circular and subacute at the apex, ca 1-1.5 mm in diam, ciliolate; petals 3, light yellow to orange-yellow, oblong-spatulate, 9-10 mm long, the center one ca 3.5 mm wide and ± cucullate at the apex, the lateral ones ca 2-2.5 mm wide, the apex ciliate; stamen 7-9.5 mm long, the filament 1.5-4 mm long, the anther basifixed, oblong, obtuse, 4-5.5 mm long, sparsely hairy at the base; staminodes ligulate, ca 1 mm long; style cylindrical, 6.5-10 mm long, glabrous, the stigma lateral. *Capsule* obtuse or subretuse at the apex, 1.7-2.5 cm long, verruculose, the seeds up to 2.3 cm long (wing included), with the limb tomentose.

From Nicaragua to Panama, and northern South America; mostly in forests; called *yemeri mayo* (cf. *Stern & Chambers 104*) in Panama.

BOCAS DEL TORO: shores of Laguna de Chiriquí, alt 150 ft, *Stern & Chambers 104* (F, MO, US). CANAL ZONE: nr Fort San Lorenzo, *Johnston 1592* (MO); Monte Lirio, *Christopherson 167* (US); Barro Colorado I, *Aviles 951* (F), *Bangham 452* (F, US), *Harvey 5283* (F), *Shattuck 847* (F, MO, US); nr Chiva-Chiva trail, *Lindsay 326* (US); Black Swamp nr Lion Hill, *Christopherson in Pittier 3790* (US); Red Tank, *Johansen 82* (US); betw Panama City & Corozal, alt 20-30 m, *Pittier 4442* (F, MO, US); Ancon Hill, alt 100-200 m, *Killip 12097* (US), *Standley 25157* (US). CHIRIQUÍ: vic of San Felix, alt 0-120 m, *Pittier 5743* (US). COCLÉ: vic of El Valle, alt 600-1000 m, S rim, dry, *Allen 1767* (F, MO, US); hills S of El Valle de Antón, alt 700 m, *Allen 2507* (US); nr El Valle de Antón, dry forest, *Alston 8829* (US). COLÓN: betw France Field, Canal Zone, & Catival, brushy slope, *Standley 30277* (US). PANAMA: Cerro Campana, *Hayden 113* (MO); Arraijan, alt 50 m, *Allen 731* (F, MO, US); vic of Arraijan, *Allen 1764* (F, MO, US); vic of Natl Airport, alt 50 ft, *Allen 4459* (MO); Cerro Azul, *Blum 3583* (MO), *Dwyer 1490* (MO). PROVINCE UNKNOWN: *Andersson s.n.* (F, MO, US).

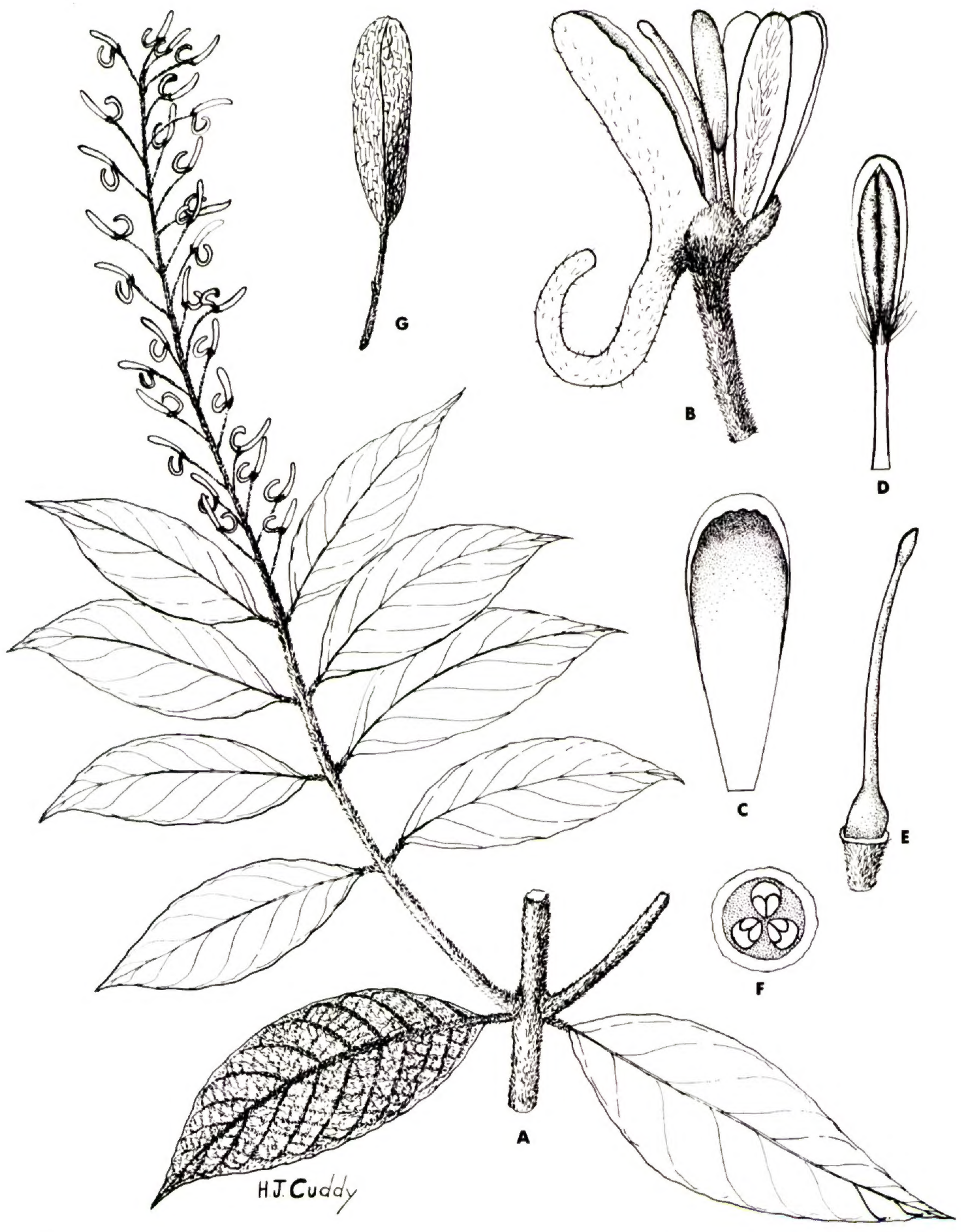

Fig. 1. *Vochysia ferruginea* Mart.: A, habit (×½); B, flower (×6); C, center petal from inside (×4); D, stamen (×4); E, gynoecium (×4); F, ovary, cross-section (×13); G, capsule (×1). A-F after *Tyson 3802* (MO); G after *Johnston 1592* (MO).

2. **Vochysia hondurensis** Sprague, Kew Bull. **1922:** 183, 1922; Stafleu, Rec. Trav. Bot. Néerl. **41:** 465, 1948.

Vochya hondurensis (Sprague) Standley, N. Amer. Fl. **25:** 303, 1924.

Tree up to 25 m tall (the only Panamanian specimen 5-6 m tall), the young branchlets angular, glabrous or almost so. *Leaves* 3-4-verticillate, the petiole slender, canaliculate above, 1-2.5 cm long, glabrous or tomentose in the groove,

the stipules 1-2 mm long, tardily deciduous; blade narrowly obovate-oblong to narrowly obovate-elliptic, attenuate-cuneate and ± decurrent at the base, rounded or obtuse and usually ± retuse at the apex, 6-15 cm long and 2-5 cm wide, the upper surface almost shining, with the midvein impressed, glabrous or the base of the midvein tomentose, the lower surface dull, glabrous or almost so. *Inflorescences* terminal and axillary, elongate-cylindrical, many-flowered, the cincinni 2-5-flowered, the rachis as the peduncles and pedicels glabrous or sparsely puberulous, the peduncles and pedicels ca 4-8 mm long. *Flowers* with the spurred calyx lobe fleshy, cucullate at the apex, glabrous or almost so, ca 9-12 mm long (without spur) and 4-5 mm wide, the spur straight or only slightly arcuate, ca ½-⅔ as long as the lobe, the other lobes subcircular, subacute at the apex, ca 1.5-3 mm long and 1.5-2 mm wide, sparsely and minutely puberulous, minutely ciliolate at the apex; petals 3, yellow, obovate, ca 4-5 mm long and 3-4 mm wide, ciliate at the apex; stamen ca 9-10 mm long, glabrous, the anther ca 5-6 mm long; staminodes ligulate, ca 1-1.5 mm long; style ca 9 mm long, glabrous, the stigma terminal. *Capsule* acute to subacute at the apex, 3-4.5 cm long, verruculose.

From Mexico to Panama.

I have seen only one collection, in fruit, from Panama, Province of Chiriquí, but, according to Standley (Contr. U. S. Nat. Herb. **27:** 229, 1928), it occurs also in the region of Bocas del Toro, "where it is said to be known as *yamery*".

CHIRIQUÍ: vic of San Bartolomé, Peninsula de Burica, alt 0-50 m, *Woodson & Schery 876* (F, MO).

2. QUALEA

Qualea Aubl., Hist. Pl. Gui. Fr. 5, 1775.

Trees or shrubs, the buds often perulate. *Leaves* opposite or subopposite, petiolate, the stipules usually represented by crateriform glands, sometimes fully developed and with similar glands at the base or provided with extrafloral nectaries; blade rigid-chartaceous to coriaceous, the midvein prominent on the lower surface. *Inflorescences* of axillary, few-flowered cincinni, or terminal and axillary, thyrsoid and with cincinni or infrequently dichasia as partial inflorescences, sometimes flowers axillary and solitary. *Flowers* with the calyx lobes unequal, one of the lateral lobes (the fourth lobe) larger than the others and usually spurred at the base, the spur sometimes saccate, the other lobes varying in size but always smaller, the lobes lateral to the spurred one (the first and second ones) usually the smallest; corolla variously colored, the petal 1, alternating with the third and fifth sepals, well developed, membranous; stamen opposite the fifth sepal, the anther basi- or dorsifixed; staminodes often present, small; ovary superior, densely pilose, 3-locular, the ovules biseriate, up to 12 per locule. *Capsules* with rounded or obtuse angles, 3-celled, the pericarp ligneous; seeds few per cell, alate, the wing unilateral, consisting of numerous, long hairs inserted on the chartaceous testa.

A neotropical genus of about 60 species, restricted to tropical South America, but with one northern range extension into the dense forests of eastern Panama; monographed by Stafleu in 1953 (Acta Bot. Neerl. **2:** 144-217).

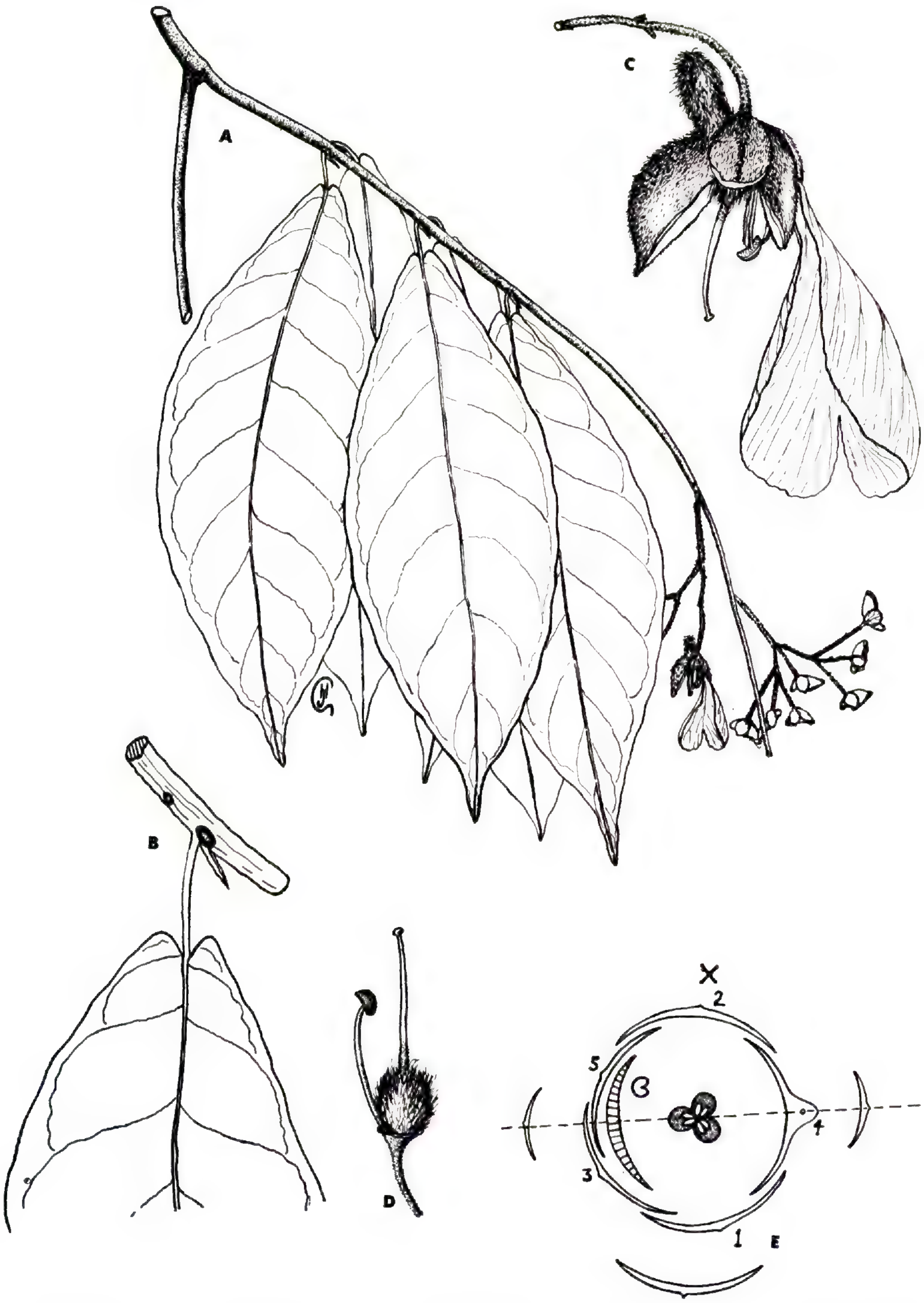

Fig. 2. *Qualea cymulosa* Schery: A, habit (×½); B, detail of leaf-base (×1½); C, flower (×2); D, androecium and gynoecium (×2); E, flower diagram. After *Allen* 4645 (MO).

1. **Qualea cymulosa** Schery, Ann. Missouri Bot. Gard. **36:** 285, 1949; Stafleu, Acta Bot. Neerl. **2:** 202, 1953.—Fig. 2.

Tree 30-50 m tall, the trunk 37.5-45 cm in diam, the branchlets minutely puberulous when young, becoming glabrous and lenticellate. *Leaves* opposite or subopposite, the petiole canaliculate above, 5-10 mm long, minutely puberulous, the stipules 3-4 mm long, the stipular glands crateriform with the margins light brownish, with 2 smaller accessory glands 1-3 mm below the main ones; blade elliptic, narrowly elliptic or narrowly elliptic-obovate, attenuate and asymmetrically subcordate at the base, rather abruptly long-acuminate at the apex, up to 15 cm long and 6 cm wide, rigid-chartaceous, glabrous except the very minutely puberulous midvein on both sides and the pubescent axils of the major lateral veins below. *Inflorescences* mostly terminal, thyrsoid with dichasia (3-flowered cymes) as partial inflorescences, the rachis as the peduncles and pedicels minutely puberulous, the pedicels up to 15 mm long. *Flowers* with the calyx cinereous-puberulous, the spurred lobe conically conduplicate-convolute, ca 9-10 mm long (without spur), the spur saccate, ca 5-6 mm long, the 2 lobes adjacent to the spurred one ± circular and 4-5 mm long, the 2 remaining lobes broadly obovate, ± convolute, ca 7-8 mm long; petal rose-pink, purple in age, very broadly obovate, deeply obcordate, shortly unguiculate, ca 2.5 cm long and wide, the claw shortly sericeous outside; stamen glabrous, the filament ca 8 mm long, the anther dorsifixed somewhat above the base, ca 2-2.5 mm long; ovary with the style glabrous except at the base, the stigma capitate. *Capsule* (according to Stafleu, loc. cit.) ca 5 cm long, the valves oblong, obtuse on both sides, the exocarp minutely verruculose and ca 3 mm thick, the endocarp thin, the 3 valves remaining connate at the base after dehiscence.

Province of Darien, Panama, and adjacent Colombia.

DARIEN: headwaters Río Chico, alt 500-750 ft, *Allen 4645* (holotype MO, isotypes F, US); trail Paya to Pucro, *Stern et al. 227* (MO, US); vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 839* (MO, US).

Index of Latin Names

Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 96A. DICHAPETALACEAE[1]

BY WALTER H. LEWIS

Missouri Botanical Garden and Department of Botany, Washington University, St. Louis, Missouri

Trees, shrubs, or infrequently woody vines. *Leaves* simple, alternate, the blade pinnately veined, entire, the stipules usually deciduous. *Inflorescences* corymbose-cymose or subcapitate, usually axillary, the peduncle often coalescent with the petiole; bracts small and linear, deciduous. *Flowers* fasciculate, small, ☿ or infrequently ♀ ♂, actinomorphic or somewhat zygomorphic, the pedicel short; sepals 5, distinct or partially connate, sometimes unequal, imbricate; petals 5, separate and equal or connate and unequal, clawed, often narrow, bifid or bilobed; stamens 5, all or only 3 fertile, alternating with disk glands, distinct or adnate to the corolla tube; disk glands separate or united into a disk, opposite the petals; ovary superior, 2-3-locular, the ovules paired at the top of the loculi, pendulous, anatropous; styles 2-3, distinct or connate nearly to the apex, often recurved, the stigma capitate or simple. *Fruit* a drupe, sometimes hispid, dry or rarely fleshy, exocarp thin, endocarp hard; seeds 1-2, pendulous, without endosperm; embryo large, straight.

A tropical, rarely extratropical, family of four genera of which only the large and widely distributed genus *Dichapetalum* is found in Panama.

1. DICHAPETALUM

Dichapetalum Thouars, Gen. Nov. Madag. 23, 1806.

Symphyllanthus Vahl, Skr. Nat. Selsk. Kjøb. **6:** 86, 1810.

Trees or shrubs, erect or scandent. *Leaves* petiolate, the paired stipules linear or narrowly lanceolate. *Inflorescences* often laxly cymose-corymbose, few- or usually many-flowered, arising from axils of upper leaves or rarely terminal. *Flowers* regular, mostly white, short-pedicellate; sepals usually distinct, ± equal; petals distinct, equal; stamens usually fertile, distinct, ± equal, the anthers broadly oblong; disk glands 5, opposite the petals or connate into a sinuate disk. *Drupe* coriaceous with 1, rarely 2, seeds.

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

About 100 species in the tropics and subtropics, some of which in Africa are poisonous. Lundell (Wrightia **3:** 173-176, 1966) recognized five species from Mexico and Central America with two in Panama.

a. Tree to 9 m; leaf blades oblong to oblanceolate, widest to 5 cm, the margins glabrate; petioles and young branches pilose with hairs less than 1 mm long and appressed; disk glands short and nob-like; petals bifid by ca ¼ length; styles 3, partially connate; drupe to 3.5 cm long, white-tomentulose .....1. *D. axillare*

aa. Shrub to 2.5 m; leaf blades linear-oblong, widest to 3 cm; blade margins, petioles and young branches velutinous-pilose, with stiff hairs ca 2 mm long and spreading; disk glands elongate; petals bilobed by more than ½ length; styles 2, distinct; drupe to 1.5 cm long, brown-tomentulose .....2. *D. nevermannianum*

1. **Dichapetalum axillare** Woodson, Ann. Missouri Bot. Gard. **29:** 353, 1942.— Fig. 1.

D. brenesii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **23:** 13, 1943.

Trees to 9 m; young branches densely pilose with hairs less than 1 mm long and appressed, glabrate with age. *Leaves* with blades oblong to oblanceolate, 9-15 cm long, 2.5-5 cm wide, membranous, the apex acuminate, the base acute, glabrous excepting the pilose veins above and below; petioles to 1 cm long, pilose, the hairs ± appressed, whitish. *Inflorescences* axillary or infrequently terminal, many-flowered, densely ash-gray-tomentulose, the peduncle to 1.5 cm long, branched, often adnate to the petiole. *Flowers* ☿, white, the pedicel short; sepals 5, ovate, ca 3 mm long, glabrous within, ash-gray-tomentulose without; petals 5, ca equalling sepals in length, narrowly ovate, moderately revolute, apically bifid by ca ¼ length; stamens 5, as long as and alternate with the petals, the filament free, glabrous, the anther very small; disk glands 5, very small, nob-like, opposite the petals; ovary ovoid, densely pilose; styles 3, to 2 mm long, partially connate, recurved, the stigma ± capitate. *Drupes* oblong-ellipsoid, to 3.5 cm long, white-tomentulose; seed 1.

Chiefly in the mountains of Costa Rica and Panama. The species is related to D. *donnell-smithii* Engler from Mexico to El Salvador and to *D. odoratum* Baillon from South America to which the San Blas collection (*Pittier 4349*) may ultimately prove to belong.

CHIRIQUÍ: Progreso, *Cooper & Slater 172* (F, NY, US). COCLÉ: hills N of El Valle de Antón, alt 1000 m, *Allen 2202* (holotype MO, isotype US). SAN BLAS: hills of Sperdi, nr Puerto Obaldia, alt 20-200 m, *Pittier 4349* (F).

2. **Dichapetalum nevermannianum** Standley & Valerio, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 597, 1937.

Shrub to 2.5 m, slender; young branches densely velutinous-pilose, the hairs ca 2 mm long, light brown, spreading at right angles to branchlets, glabrate with age. *Leaves* with blades linear-oblong, 7-13 cm long, 1.5-3 cm wide, the apex narrowly attenuate, the base ± unequal, broadly rounded or slightly cordate, velutinous-pilose above and below chiefly on the mid-vein and margin; petioles to

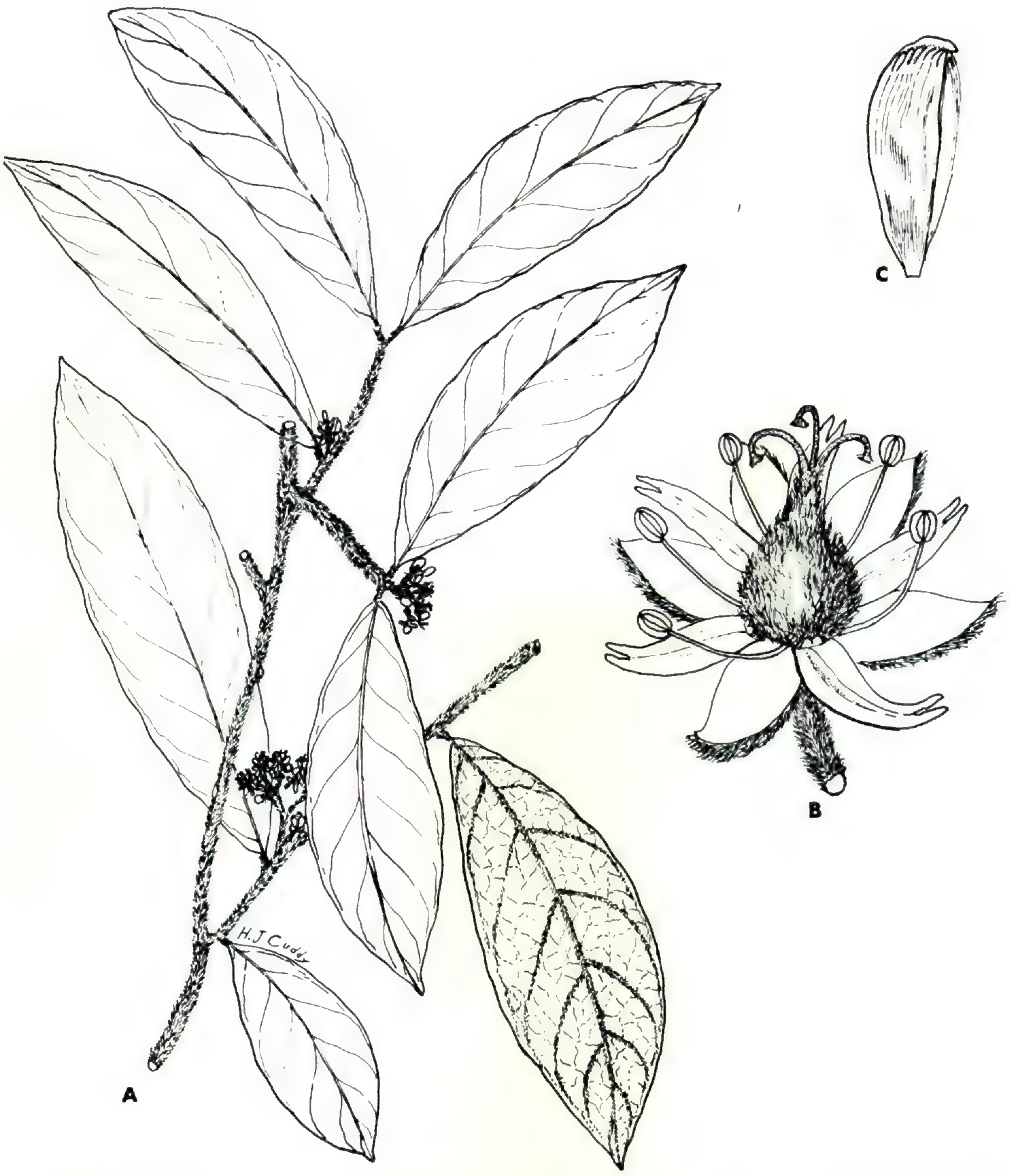

Fig. 1. *Dichapetalum axillare* Woodson: A, habit (×½); B, flower (×5); C, fruit (×1). A-B after *Allen 2202* (MO); C after *Brenes 6766* (F), Costa Rica.

5 mm long, densely velutinous-pilose, the hairs spreading, light brown. *Inflorescences* usually terminal, few-flowered, densely ash-gray-tomentulose, the peduncle ca 5 mm long. *Flowers* ☿, white, the pedicel very short; sepals 5, oblong to oval, 2-3 mm long, glabrous within, ash-gray-tomentulose without; petals 5, ca equalling sepals in length, clawed, strongly revolute, bilobed by more than ½ length; stamens 5, somewhat longer than petals, subequal, the filament free, glabrous, the anther ca 0.5 m long; disk glands 5, ca 1-1.5 mm long, elongate, opposite the petals; ovary narrowly ovoid, densely pilose, ca 1.5 mm long; styles 2, 0.5 mm

long, free, erect, the stigmas 2, rarely 3, ± capitate. *Drupes* ovoid, 12-15 mm long, densely brown-tomentulose; seed 1.

Rarely collected in lowland forests on the Caribbean side of Costa Rica and Panama. The species is one of the most distinct in the Americas.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Water Valley, *von Wedel 1424* (F, MO).

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Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 100. CORIARIACEAE[1]

BY CALAWAY H. DODSON[2]

University of Miami, Coral Gables, Florida

Suffrutescent perennial *herbs,* shrubs, or rarely small trees, the branchlets angular, the lower ones opposite or ternate, the upper ones opposite. *Leaves* opposite, rarely whorled, sessile, simple, entire, (1-)3-5-nerved from base, estipulate. *Inflorescences* terminal on axillary branchlets, racemose, or sometimes flowers axillary and solitary. *Flowers* ☿ or subpolygamous, actinomorphic, very small, the perianth biseriate; sepals 5, imbricate, persistent; petals 5, hypogynous, shorter than the sepals, fleshy, carinate within, thickened after anthesis and intruded between the cocci to produce a pseudodrupe; stamens 10, hypogynous, distinct, or the 5 opposite the petals adnate to the keel of the petals, the filaments short and filiform; anthers rather large, exserted, oblong, 2-celled, longitudinally dehiscent; gynoecium of 5-10 distinct carpels, these adnate in a whorl around the fleshy conic torus, 1-celled, the ovules solitary, pendulous from the apex of the cell, anatropous; styles as many as the carpels, free, elongated, usually divergent, stigmatose all around. *Fruits* of 5-10 cocci included in the accrescent petals, compressed, oblong; seeds compressed; endosperm scanty; embryo straight.

One genus with eight species, only one in the New World tropics.

CORIARIA

Coriaria L., Gen. Pl. ed. 5, 459, 1754.

Characters of the family.

The members of this genus are extremely poisonous to livestock and serious illness or death has been reported in children who have eaten quantities of the sweet fruits. Heavy losses of livestock have been reported in New Zealand due to eating the leaves of a species of this genus, and cattle are poisoned in the Andes area of South America.

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2] I wish to express thanks and appreciation to the curators of the following herbaria for the loan of specimens and facilities of study: Field Museum of Natural History, Chicago, Illinois (F), New York Botanical Garden (NY), and U. S. National Herbarium, Washington, D. C. (US).

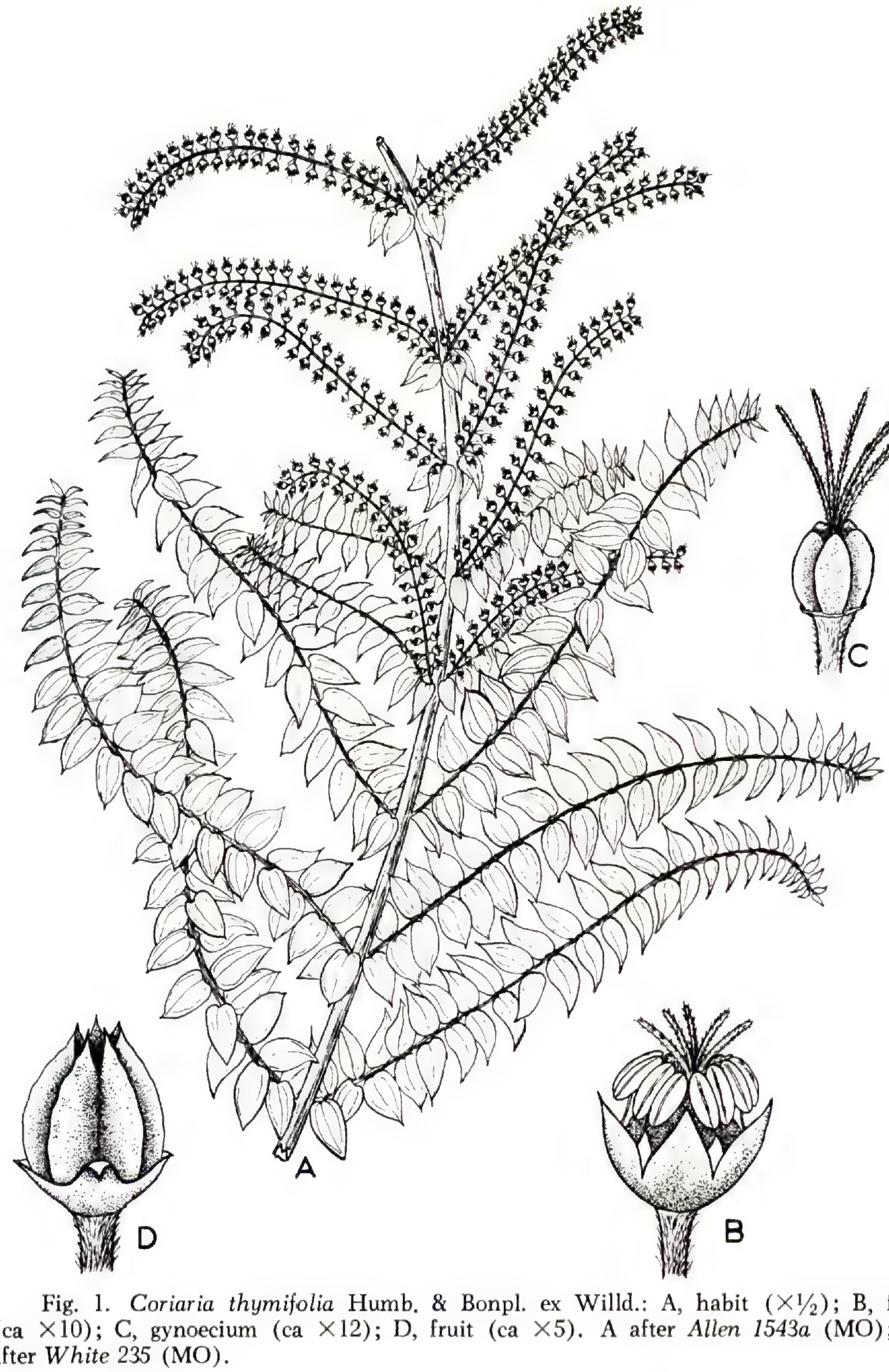

Fig. 1. *Coriaria thymifolia* Humb. & Bonpl. ex Willd.: A, habit (×½); B, flower (ca ×10); C, gynoecium (ca ×12); D, fruit (ca ×5). A after *Allen 1543a* (MO); B-D after *White* 235 (MO).

1. **Coriaria thymifolia** Humb. & Bonpl. ex Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **4:** 819, 1806.—Fig. 1.

Slender *shrub,* often sarmentose, commonly 1-4.5 m high, usually recurving, the branches green or in age brownish. *Leaves* all spreading in one plane, closely

set, sessile or nearly so, lanceolate-oblong to oblong-ovate, acute or subacute at the apex, truncate to cordate at the base, subcoriaceous, conspicuously nerved, 1-2 cm long, 5-15 mm broad, glabrate or glabrous. *Racemes* apical on small lateral branchlets, virgate, 4-10 cm long, arcuate, slender-pedicellate. *Flowers* 2 mm long, yellow, green or dark red; sepals triangular-ovate, 1 mm long, 0.5 mm broad, glabrous; petals triangular, 1-1.5 mm long, glabrous; stamens yellow; styles terete, exserted conspicuously from the flower. *Fruits* globose, 3-4 mm thick, juicy, dark purple.

Central Mexico, through Central America to the Andes in South America, usually at higher elevations.

CHIRIQUÍ: Llanos del Volcán, alt 1300-1600 m, *Allen 1543a* (F, MO, NY, US), *Allen & Fairchild 3461* (MO, NY, US); Volcán de Chiriquí, Potrero Muleto, alt 10,400 ft, *Davidson 1013* (F, MO, US); betw El Hato (Volcán) & Cerro Punta, llanos, *Ebinger 800* (MO); Volcán de Chiriquí, ca peak, alt 11,000 ft, *Terry 1329* (F, MO, US); 5 mi NE of El Volcán, alt ca 6300-6500 ft, in dry arid canyon bottom, *Tyson 806* (MO); valley of upper Río Chiriquí Viejo, Cerro Pando, *White 46* (MO); Río Chiriquí Viejo valley, nr El Volcán, *White 235* (F, MO); Volcán de Chiriquí, Potrero Muleto, alt 3500-4000 m, open slopes, *Woodson & Schery 416* (MO, US); id, Loma Larga to summit, alt ca 2500-3380 m, on rim of crater, *Woodson et al. 1059* (F, MO, NY)

This widely distributed species is often encountered growing along roadsides and stream banks in the cloud forest regions. At first glance it gives the impression of being a large fern. It is quite attractive and is often used by the natives as greenery in flower arrangements at the numerous roadside shrines. The juice of the purple fruits is occasionally used as ink.

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Numbers in **boldface** type refer to descriptions.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 101A. CYRILLACEAE[1]

BY THOMAS S. ELIAS

Saint Louis University, St. Louis, Missouri

Shrubs or small trees, rarely large trees. *Leaves* simple, estipulate, moderately to heavily coriaceous, glabrous to pubescent, the venation usually pinnate, strongly arcuate in some *Prudiaea*. *Flowers* in terminal or axillary racemes; bracts lanceolate to deltoid; sepals 5 (-6-8), rarely united, deltoid and equal or variable and unequal, persistent; petals 5 (-6), membranaceous, white to pinkish-white or deep pink to violet, shortly connate; stamens 5 or 10, hypogynous, the filaments free; anthers 2-locular, dehiscing longitudinally or by terminal pores; pollen 3-4-colporate; ovary superior, 2-5-locular, the style short, the stigmas 1-3 (-4). *Fruit* a capsule or drupe, sometimes winged, frequently without seeds; seeds without a seed coat.

A tropical family of three genera and 13 species with only one genus represented in Panama. This family was not known from Panama until a single collection was made in 1966.

1. CYRILLA

Cyrilla Garden ex L., Mant. Pl. **1:** 5, 1767.

Shrubs or trees. *Leaves* entire, short-petioled, subcoriaceous to coriaceous. *Flowers* with the sepals equal; petals white, thickened and glandular medially and below the middle; stamens 5, dehiscing longitudinally, the filaments terete, subulate; styles short, 2-3-lobed. *Fruit* a drupe, longitudinally bisulcate or trisulcate.

A monotypic genus.

1. **Cyrilla racemiflora** L., Mant. Pl. **1:** 50, 1767.—Fig. 1.

Trees (in Panama) with thick, rough, brown bark; diam ca 45 cm; branches glabrous, terete; branchlets subterete to angulate, glabrous. *Leaves* crowded towards the ends of the branches, the blade oblanceolate, narrowly cuneate at base, acute to subobtuse at apex, recurved marginally, coriaceous, glabrous, the midvein prom-

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

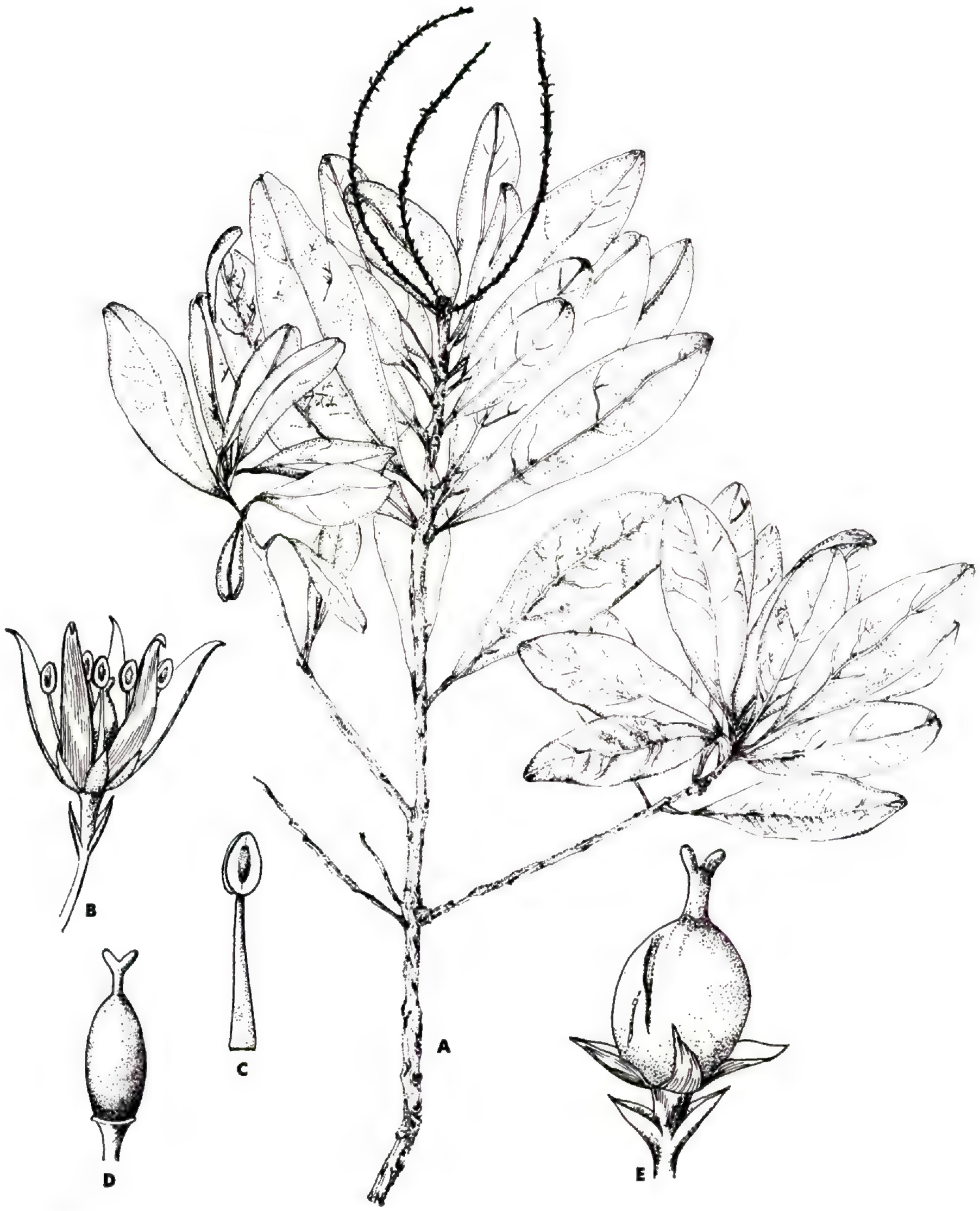

Fig. 1. *Cyrilla racemiflora* L.: A, habit (×½); B, flower (×6); C, stamen (×10); D, pistil (×10); E, fruit (×10). A & E after *Blum & Duke 2180* (MO); B-D after *Tracy 8721* (MO), Florida.

inent beneath, densely reticulate, 2-9 cm long, 1-2.4 cm broad; petiole to 4 mm long, glabrous. *Racemes* 3.5-10 cm long, borne in the upper axils, erect to pendulous, glabrous; peduncles 4-10 mm long, glabrous; bracts 0.5-1.5 mm long, lanceolate, glabrous, persistent, ascending in bud, spreading to descending after anthesis. *Flowers* ascending in bud, spreading at anthesis, pedicellate, the pedicel 1-2 mm long, glabrous; bracteoles paired, alternate to opposite, 0.5-1 mm long, lanceolate, basally thickened, usually persistent, borne above the middle of the pedicel, spread-

ing after anthesis; sepals 5, free, ovate-lanceolate to deltoid, acute at apex, 0.4-0.7 mm long, imbricate in bud; petals 5, inserted on a small glandular disk, oblong-lanceolate to oblong-elliptic, acute at apex; stamens opposite the petals, 1.5-2 mm long, the filaments terete, the anthers versatile; ovaries sessile, 2-3(-4)-locular, the style persistent, the stigma 2-4-lobed. *Fruits* dry, globose, ovoid to oblong-ovoid, 1.6-2.7 mm in diam; seeds elongate; cotyledons short, inferior; radicle superior.

This species is widely distributed in southeastern United States, the West Indies, British Guiana, Venezuela and is known from northwestern Brazil and southeastern Colombia. Previously the only reported collections in Central America were from Oaxaca, Mexico and British Honduras.

PANAMA: E slope of Cerro Jefe, *Blum & Duke 2180* (MO).

Since the Panamanian material of *C. racemiflora* has only been collected in fruit, most of the floral descriptions have been taken from the recent monograph of the family by Thomas (Contr. Gray Herb. Harvard Univ. **186:** 77-104, *fig. 24-41, map,* 1960). Information concerning the variation and synonymy of this species is available in the monograph. A chromosome number of $n = 20$ in most cells was reported by Thomas (loc. cit. 25) from specimens from northern Florida.

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Numbers in **boldface** type refer to descriptions; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 110. BALSAMINACEAE[1]

BY THOMAS S. ELIAS

Saint Louis University, St. Louis, Missouri

Herbs, rarely shrubby, annual or perennial, occasionally epiphytic or aquatic; stems usually succulent and often swollen at the nodes, glabrous or with simple hairs. *Leaves* simple, alternate, opposite, verticillate or spirally arranged, the margins entire, crenulate, serrate or denticulate, occasionally with tentacular hairs on the apex of the crenations, usually petiolate, often with marginal petiolate hairs; stipules absent. *Inflorescences* usually axillary, rarely of terminal racemes, pseudoumbels, fascicles, or flowers solitary. *Flowers* zygomorphic, perfect, brightly colored, sometimes cleistogamous; sepals 3, rarely 5, often colored, deciduous, imbricate, unequal, the lateral sepals varied, usually small, green or colored, the lowermost or posterior sepal elongated, tubular, often saccate or conic, usually with a tapering spur; petals 5, rarely free or 3 by union of 2 pairs of lateral and posterior petals, the lateral petals usually deeply 2-lobed, variable in shape, the upper or anterior one exterior, usually erect, always large, flat or helmet-shaped; stamens 5, alternate with the petals, the filaments short and thickened, connate near the apex; anthers 2-thecate, connate around the ovary; ovary superior, 5-locular with axile placentation; stigmas 1-5, more or less sessile; ovules ∞, pendulous, anatropous. *Fruit* a succulent capsule, dehiscing elastically into 5 twisted valves, rarely a berry; seeds with a dorsal raphe, without endosperm.

Mainly of tropical Asia and Africa; the family is composed of the large genus *Impatiens* (more than 500 described species) and the monotypic genus *Hydrocera* of Indo-Malaysia.

1. IMPATIENS

Impatiens L., Sp. Pl. 937, 1753.

Annuals in our species; stems glabrous. *Leaves* serrate to crenate-denticulate, petiolate. *Inflorescences* axillary. *Flowers* pedicellate; sepals 3; the lateral petals connate in pairs. *Fruit* an elastically dehiscent, glabrous or pubescent capsule.

Widely distributed in the Old World tropics with only a few species in the more temperate regions of the New World. Several species are often grown as

[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

ornamentals. In Panama two species occur, one native and a possible escape; a third species, *I. balsamii,* is probably grown as an ornamental in Panama, but no collection has been seen.

a. Leaves opposite, the margins serrate toward the apex, without hairs on the apex of the serrations; posterior sepal gradually spurred, the spur tapering, incurved .....1. *I. turrialbana*

aa. Leaves alternate, the margins crenate-denticulate with tentacular hairs on the apex of the crenations; posterior sepal abruptly spurred, the spur slender, slightly curved .....2. *I. wallerana*

1. **Impatiens turrialbana** J. D. Sm., Bot. Gaz. **23:** 241, 1897.—Fig. 1.

Herb, erect, often branched, somewhat succulent; stems striate. *Leaves* opposite, uppermost crowded to appear whorled, the blade elliptic to oblong-elliptic, glabrous, 2-7.5 cm long, 1-3 cm broad, serrate toward the apex, entire toward the base, obtuse to subacute at apex, mucronate, short-cuneate at base; lateral veins 8-12 pairs, ascending, inconspicuous; petioles 1-4 cm long, glabrous. *Inflorescences* racemose, borne singly in the upper axils, usually 2-flowered; peduncles 4-5 cm long, glabrous. *Flowers* scarlet, with the pedicels 16-19 mm long, with a single bract about midway, the bract 3-4 mm long, deltoid, clasping, apiculate, glabrous; lateral sepals to 8 mm long, 7 mm broad, circular, ovate, apiculate, subcordate at the base; posterior sepal to 2-3 cm long (including the spur), saccate, horn-like, inflated at the apex, gradually spurred, the spur incurved, unspotted; anterior petal to 10 mm long and broad, broadly ovate to broadly oblong, usually apiculate; lateral petals united, oblong-elliptic with 2 oblong or ovate lobes to 4 mm long, 3-4 mm broad; ovary usually glabrous. *Capsules* to 2.5 cm long, clavate, 2-3 mm in diam, glabrous; seeds not seen.

CHIRIQUÍ: valley of upper Río Chiriquí Viejo, *White* 69 (MO).

Impatiens turrialbana, the only native species in Central America, exclusive of Mexico, was believed endemic to the slopes of Turrialba and Irazu in Costa Rica.

2. **Impatiens wallerana** Hook. f. in Oliv., Fl. Trop. Afr. **1:** 302, 1868.

Impatiens sultani Hook. f., Curt. Bot. Mag. **108:** *t.* 6643, 1882.

Herb, erect, usually branched, rather succulent; stems terete, thick, glabrous, usually striate, usually translucent, minutely white spotted. *Leaves* alternate, spirally arranged, often crowded above, the blade broadly elliptic or ovate, usually translucent, glabrous, 2.5-10 cm long, 1.3-5 cm broad, acute to short-acuminate at the apex, marginally crenate-denticulate with tentacular hairs on the apex of the crenations, narrowly cuneate at base, often forming a narrow wing on the petiole, with 7-12 pairs of ascending, inconspicuous, lateral veins; petiole 1-3 cm long, usually glabrous, with 1-several marginal tentacular hairs, the hairs to 1 mm long, flattened at the apex. *Inflorescences* of few-flowered racemes; peduncles 4-5 cm long, glabrous. *Flowers* usually dark, carmine, red, pink, orange, or violet, with

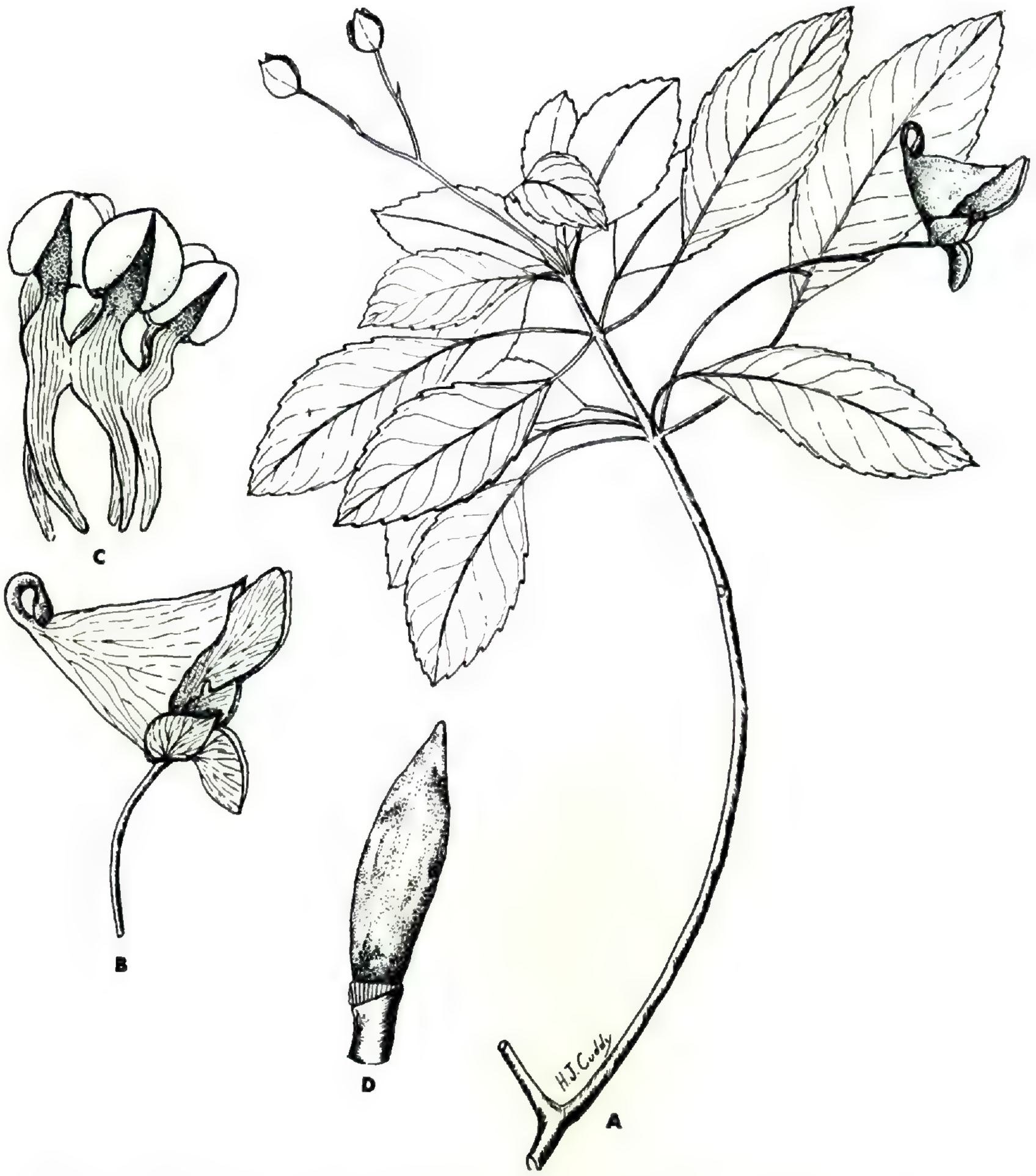

Fig. 1. *Impatiens turrialbana* J. D. Sm.: A, habit (×1); B, flower (×2); C, stamens (×14); D, immature capsule (×10). A after *White 69* (MO); B-D after *Cox 4758* (US), Costa Rica.

the pedicel 2-2.2 cm long, glabrous, with a pair of linear-lanceolate bracts at the base of the pedicel, the bracts to 3 mm long, glabrous; lateral sepals 4-7 mm long, 2-3 mm broad, ovate-lanceolate, acute, usually glabrous, green; posterior sepal to 1.5 cm long, shallowly navicular, abruptly constricted into the spur, the spur up to 4 cm long, slender, slightly curved, glabrous; anterior petal to 12 mm long, up to 18 mm broad, broadly ovate or obcordate, usually retuse to emarginate at the apex; lateral petals united, very deeply 2-lobed, the lobes equal in size and shape, 1.5-2 cm long, 1.2-1.4 cm broad, obovate, rounded or subtruncate at apex; ovary usually glabrous. *Capsule* to 18 mm long, fusiform, glabrous; seeds numerous, ca 1.5 mm in diam, pyriform, blackish, usually covered with short thick hairs.

PANAMA: Cerro Azul, *Tyson 2189* (MO).

A native of eastern tropical Africa this species is commonly cultivated in Central America. It has been erroneously reported from Central America as *I. sultani* (Fieldiana: Bot. **24** (6): 277, 1949); however, this species should properly be placed in synonymy with *I. wallerana*.

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Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 119. OCHNACEAE[1]

BY JOHN D. DWYER

Missouri Botanical Garden and Department of Biology, Saint Louis University,
St. Louis, Missouri

Trees, shrubs, or herbs. *Leaves* sessile or petiolate, simple (extra-Panama rarely compound), stipulate. *Inflorescences* terminal or axillary, racemose or cymose, the flowers rarely solitary. *Flowers* ☿, actinomorphic; sepals usually 5, occasionally reduced to 4 or up to 10; petals usually the same number as the sepals, mostly imbricate in the bud; stamens 5 to ∞, hypogynous, often surrounded by one to several rows of staminodia, the anthers basifixed, dehiscing poricidally or longitudinally; pistil solitary, the ovary superior, often borne on an enlarged torus or gynophore, the carpels and locules 2-5, the placentae axile or parietal, intrusive, the ovules ∞ (rarely 1 per locule), occasionally alate, the style usually slender and unbranched, the stigmatic surface often indistinguishable or the stigmas radial and conspicuous. *Fruits* either baccate, the carpels separating as distinct cocci or druplets on an enlarged torus, or capsular and dehiscing septicidally, or rarely nut-like and indehiscent (extra-Panama), the seeds occasionally conspicuously winged.

Pantropical, especially well represented in northeastern South America.

a. Trees or erect shrubs; flowers lacking coronal segments, yellow.
   b. Large trees with leaves up to 1 m long, clustered or whorled at the ends of the branches; panicles up to 1 m long; leaves rounded or obtuse at the apex ..... 1. *Cespedezia*
   bb. Shrubs or at most small trees; leaves up to 30 cm long, mostly well-spaced along the branches; panicles up to 20 cm long; leaves acute or acuminate at the apex ..... 2. *Ouratea*

aa. Herbs or sprawling subshrubs; flowers with an obvious interior corona, white, pink, rarely yellow ..... 3. *Sauvagesia*

1. CESPEDEZIA

Cespedezia Goudot, Ann. Sci. Nat., Bot., sér. 3, **2:** 370, 1844.

Godoya Ruiz & Pav., Fl. Peru. Prodr. **1:** 58, 1794, pro parte.
Fourneiria van Tieghem, Ann. Sci. Nat., Bot., sér. 8, **19:** 58, 1904.

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis.).

Trees, large; branches whorled and clustered at the apices of the trunk. *Leaves* with the petioles short; blades simple, glabrous, the costa prominent above and below, the lateral veins arcuate, the margin undulate, the marginal teeth minute; stipules ± persistent, densely imbricate and appressed, entire, bearing small upright fimbriae on the basal and adaxial margin. *Inflorescence* terminal, paniculate, the branches patulous, arcuate, the flowers few in well-spaced fascicles borne on short tertiary branches, the pedicels shortly articulate at the base, the bracts deciduous, bearing small upright fimbriae on the basal and adaxial margin. *Flowers* with the buds obovate or oblong; sepals 5, subequal or obviously unequal, imbricate and united into a very short cup, coriaceous, dorsally marcescent and carinate, ventrally smooth, bearing minute fimbriae on the basal and inner margin; petals 5, spreading at anthesis, the veins flabellate; stamens 50-80, in several rows, the filaments encircling the pistil basally at anthesis, the anthers deciduous, 4-celled, opening by 2 oblique terminal pores, the filaments filamentous, often longer than the anthers; pistil stipitate, secund, the ovary 1-celled, 5-carpellate, the ovules borne in several series on intrusive T-shaped parietal placentae, the style short, the stigmas 5, radially disposed, spongy. *Fruits* capsular, dehiscing septicidally, the carpels coriaceous, the placentae at dehiscence separating from the margins of the carpels, the seeds numerous, imbricate, long-winged, the corpus centrally located, the wings subequal, scarcely wider than the body of the seed.

A small genus known from Nicaragua and the southern part of Central America as well as throughout most of tropical South America.

1. **Cespedezia macrophylla** Seem., Bot. Voy. Herald 97, 1853.—Fig. 1.

Trees up to 15 m high, with aerial roots and buttresses; branches often conspicuously thickened, bearing conspicuous leafscars, the scars subrotund, up to 2 cm in diam. *Leaves* with the petioles ca 1 cm long, plane above; blades fasciculate and strongly ascending at the ends of the branches, obovate or obovate-elliptic, up to 1 m long, 18-25 cm wide, obtuse, rarely subacute at the apex, cuneate at the base, coriaceous, glabrous, the costa prominent above and below, carinate above, the lateral veins prominent, stiff, divergent, ca 1-2 cm apart in the middle, not strongly arcuate, arising from the costa at a 50°-60° angle, the tertiary veins subimmersed, conspicuously lineolate, the margin shallowly undulate, the cilia minute, falcate, up to 3.5 cm apart; stipules densely imbricate, appressed, subligneous, narrowly rectangular, up to 7 cm long and 1.3 cm wide, often splitting lengthwise, the basal adaxial fimbriae up to 1 cm long. *Inflorescences* exceeding the uppermost leaves, the branches few, patulous, widely arcuate, the flowers in fascicles of 3-4 flowers on tertiary branches, the basal branches up to 4 cm long; bracts and bracteoles deciduous; pedicels 1.3-1.5 cm long, granular-puberulent. *Flowers* with the buds elliptic, up to 2 cm long, widely acute at the apex; sepals subequal, strongly divergent at anthesis, elliptic, ca 0.5 cm long, rounded and entire at the apex, coriaceous, glabrous, the margin often minutely erose; petals yellow, obovate, up to 3 cm long, obtuse at the apex, constricted basally; stamens ca 80, the anthers ca 1 cm long, 0.5 cm wide, the filaments up to 1.3 cm long; pistil with the stipe

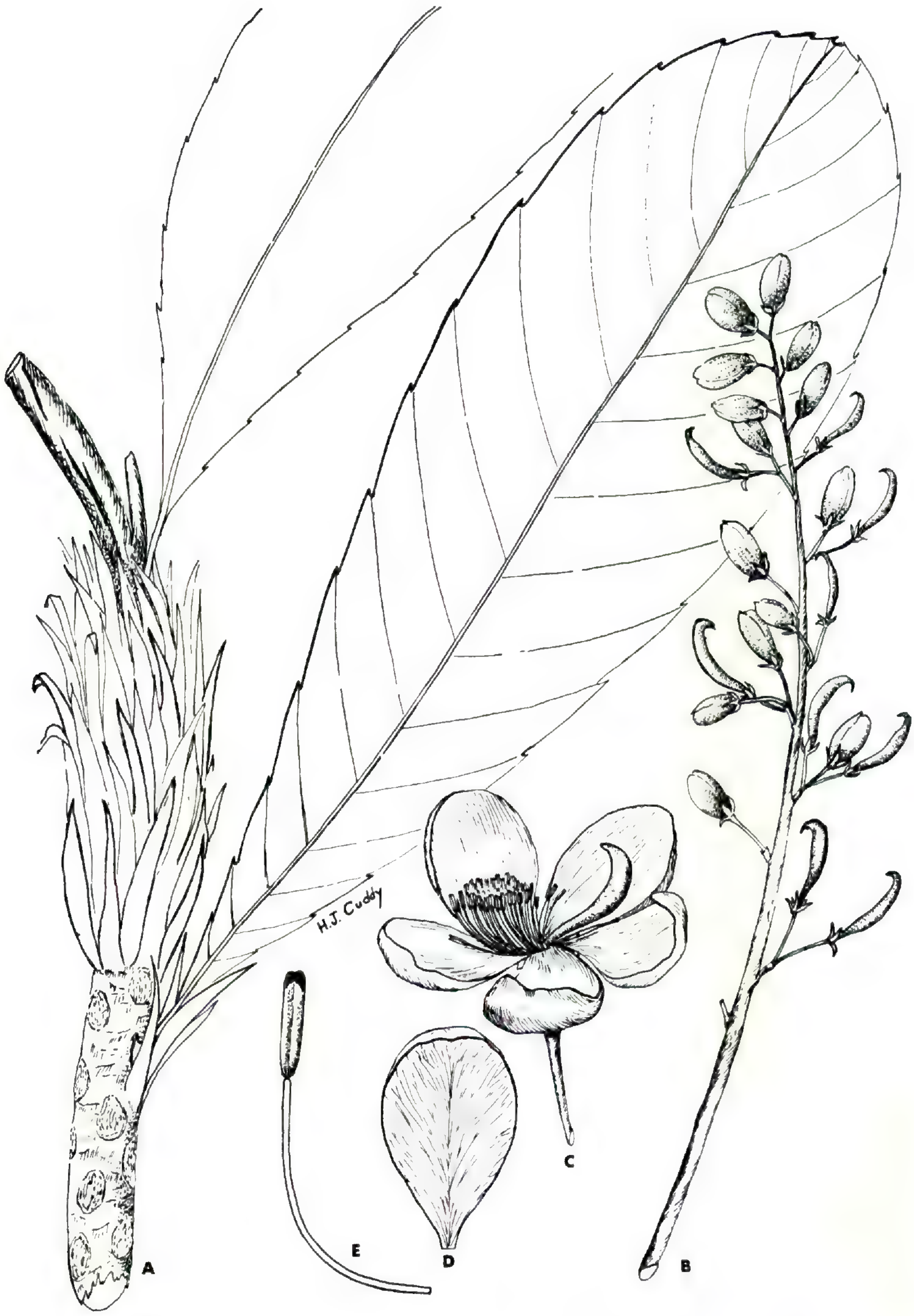

Fig. 1. *Cespedezia macrophylla* Seem.: A, habit (×1/4); B, branch of inflorescence with buds and young fruits (×1/2); C, flower (×1); D, petal, adaxial view (×1); E, stamen, adaxial view (×5). A after *Allen 2974* (MO), *5134* (MO); B after *Shattuck 791* (F, MO); C-E after *Lewis et al. 877* (MO).

up to 0.7 cm long, the ovary up to 1.3 cm long, ca 0.2 cm wide, the style scarcely measureable. *Capsules* (here immature) narrowly falcate, up to 6.5 cm long, ca 0.7 cm wide, the seeds angular, the corpus up to 1.3 mm long, the wing up to 8 mm long.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 121* (F, US); 10-15 mi S from mouth Río Changuinola, *Lewis et al. 877* (MO); Water Valley, *von Wedel 1653* (MO), *1758* (MO), *2152* (MO); Almirante, *Woodson & Schery 1030* (MO). COCLÉ: El Valle de Antón, *Allen 2974* (MO); Penonome, *Williams 424* (NY, UC). CANAL ZONE: Gatun, *Hayes 39* (MO), *s.n.* (K); nr Pina Base Camp, Fort Sherman, *Johnston 1799* (MO); Río Gatuncillo, *Allen 5134* (MO); Barro Colorado I, *Kenoyer 665* (NY); Gross Point, *Shattuck 791* (F, MO). PANAMA: Bay of Utria, *Seemann s.n.* (GH, K). SAN BLAS: Obaldia, *Pitter 4340* (NY).

When in full bloom *C. macrophylla* is one of the most conspicuous trees in the forest. Its foliage, terminally disposed in upright whorls, strongly suggests *Gustavia superba* (H.B.K.) Berg. of the *Lecythidaceae.*

2. OURATEA

Ouratea Aubl., Hist. Pl. Gui. Fr. 397, 1775, nom. gen. conserv.

Trees or shrubs. *Leaves* alternate, persistent, simple, membranaceous or coriaceous with the median nerve strongly prominent; stipules subulate, striate. *Inflorescences* terminal or axillary, paniculate or racemiform, the flowers usually disposed in well-spaced bostryces, pedicellate. *Flowers* ☿ with 5 unequal and imbricate sepals; petals 5, hypogynous, subequal; stamens 10, hypogynous, connivent; anthers subsessile, subulate, more or less rugose, dehiscing by oblique apical pore; receptacle thick, in fruit swollen or club-shaped; carpels 5-10, uniloculate, with the style central, filiform, the stigma undifferentiated. *Fruits* disposed as usually 5 druplets sessile on the swollen torus; seeds erect, exalbuminous.

Mostly in the tropics of the New World; a few species found in Asia and Africa.

The nomenclatural problem associated with the genus has been discussed by the author (Taxon **14:** 275-277, 1965).

a. Leaves not densely fasciculate, usually persistent on well developed branchlets.

b. Leaves sessile or subsessile, somewhat fasciculate and strongly ascending on branches, 35-75 cm long.

c. Leaves spatulate, deltoid and scarcely acuminate at the apex; lateral veins of the lamina rigid and not impressed above .....1. *O. curvata*

cc. Leaves obovate, rounded toward the apex, ultimately distinctly acuminate, the lateral veins arcuate and obviously impressed ....2. *O. tuerckheimii*

bb. Leaves petiolate, spreading, 5-30 cm long.

d. Inflorescences widely pyramidal-paniculate.

e. Leaves with margins finely serrate .....3. *O. insulae*

ee. Leaves with the margins entire .....4. *O. cocleensis*

dd. Inflorescences contracted, paniculate or racemiform.

f. Inflorescences 18-25 cm long.

g. Leaves ca 4× longer than wide, lateral veins ca 10, 2-3.5 cm apart, margins vaguely repand; pedicels (at least in fruit) strongly reflexed; receptacle of fruit mostly obovate .....5. *O. flexipedicellata*

gg. Leaves ca 3× longer than wide, lateral veins ca 20, up to 1 cm apart, margin serrate or serrulate; pedicels not strongly deflexed; receptacle of fruit patelliform .....6. *O. patelliformis*

ff. Inflorescences 3-10 cm long .....7. *O. lucens*

aa. Leaves densely fasciculate and soon deciduous from short lateral branches .....8. *O. mexicana*

1. **Ouratea curvata** (St.-Hil.) Engler ex Dwyer, Lloydia **7:** 128, 1944.

Gomphia curvata St.-Hil., Fl. Bras. Merid. **1:** 69, 1825.
Ouratea crassinervia Engler in Mart., Fl. Bras. **12**(2): 337, 1876.
O. costaricensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 694, 1937.

Shrubs or occasionally small trees; ultimate branches terete, usually rough with persistent stipules or petioles. *Leaves* subsessile, fasciculate, strongly ascending; petioles up to 1 cm long; leaf blades spatulate, 35-50 cm long, 6.5-12 cm wide, deltoid toward the apex, not acuminate, tapering narrowly toward the base, auriculate at the base, the lamina thinly coriaceous, glabrous, the lateral veins ca 25, prominulous (or occasionally seemingly immersed), the veins of the middle of the lamina arcuate, the lowermost 2 or 3 veins strongly ascending, the margin serrulate above the middle or along the upper ⅔, each tooth receiving a small vein from a larger vein paralleling the margin and located a few mm from the margin; stipules fasciculate, strongly ascending, deltoid, up to 1.5 cm long, acute. *Inflorescences* either solitary and terminal or with several axillary rachises below the terminal one, measuring ⅓-½ the length of the uppermost leaves, the rachis terete, 0.2-0.3 cm long, rather stout in the fruit, drying dull red-brown, glabrous, the bostryces disposed above the middle, usually few, well-spaced for 1-2 cm, the secondary branches ca 0.5 cm long, the flowers up to 3 per bostryx, the pedicels slender, up to 0.8 cm long, ca 0.4-1 mm wide; bracts scattered, occasionally persistent along the lower half of the rachis, narrowly ovate, up to 0.8 cm long; flower buds ovate, up to 0.8 cm long, shortly acuminate at the apex. *Flowers* with petals up to 10 mm long, slightly longer than the sepals. *Fruits* with the pedicels up to 1 cm long; receptacles obpyriform, 1-1.5 cm long, 0.6-1 cm wide, obtuse or truncate above, the drupes elliptic, 0.7-1 cm long, 0.5-0.7 cm wide.

Known from Costa Rica, Panama, and Brazil.

BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *von Wedel 1437* (MO), *1648* (MO); Isla de Colón, *Woodson et al. 1948* (F, MO); s. loc., *von Wedel 314* (MO).

The inflorescence of *O. curvata* has a distinct red coloration in the fresh condition; the receptacle of the fruit is bright red with the drupes shiny black.

2. **Ouratea tuerckheimii** J. D. Sm., Bot. Gaz. **23:** 194, 1902.

Shrubs or small trees; branchlets terete, glabrous. *Leaves* sessile or subsessile, fasciculate and strongly ascending, oblong or obovate-oblong, up to 75 cm long, up to 11 cm wide, usually widest just above the middle, tapering widely but obtusely toward the apex, obviously acuminate, the acumen usually acute, often narrowing gradually at the base but ultimately obtuse or subauriculate, the blade thinly coriaceous, glabrous, the lateral veins 15-20, widely arcuate, immersed above (at least when dry), often with one or two shorter and more oblique veins located between each pair of major veins, the margin regular proximally, serrulate along the upper ⅔. *Inflorescences* solitary, terminal or axillary, racemiform or obviously pyramidal-paniculate, usually ca as long as or slightly shorter than the leaf blades, the rachis unbranched or flowerless for 5-7 cm, smooth, twisted and somewhat flexuous, 0.2-0.4 cm wide, the branches 1-4, usually obviously arcuate, the lowermost branches 5-20 cm long, smooth, glabrous, the bostryces 1-2-flowered, disposed along the upper ⅔ of the branches, well-spaced, subsessile. *Flowers* with the pedicels slender, up to 1 cm long; flower buds ovate, up to 0.9 cm long, ultimately obtuse; petals up to 1 cm long. *Fruits* with the pedicels up to 1 cm long, ligneous, the receptacles oblong or oblong-rotund, up to 13 mm long, up to 9 mm wide; drupes not seen.

Known from Guatemala and Panama.

PANAMA: 7 mi N Cerro Azul on rd to Cerro Jefe, alt 2600 ft, *Blum et al. 1800* (MO); Cerro Azul, *Dwyer 1371* (MO).

3. **Ouratea insulae** Riley, Kew Bull. **1924:** 106, 1924.

Gomphia nitida Hemsl., Biol. Centr. Veg. Bot. **4:** 111, 1887, non Sw., Fl. Ind. Occ. **2:** 739, 1800.
Ouratea pyramidalis Riley, Kew Bull. **1924:** 107, 1924.

Trees 12-25 m high; twigs terete, smooth, ashen-gray. *Leaves* with the petioles 0.7-1 cm long, 1-3 cm apart; blades well-spaced, oblong-elliptic, often narrowly so, 12-31 cm long, 3.5-8 cm wide, acute and often short-acuminate at the apex, cuneate or round-obtuse at the base, lustrous, coriaceous, yellow-brown when dry, the margin serrate, often entire for 2-3 cm from base, occasionally up to the middle, the costa prominent above, often subplane above the base, prominent and longitudinally striate beneath, the lateral veins of two kinds, some (25-50) distinctly prominulous, arcuate-ascending, paralleling the margin for a distance and eventually passing into a marginal tooth, the others more numerous, crowded, irregular, immersed or prominulous, scarcely ascending. *Inflorescences* terminal, pyramidal-paniculate, the rachis stout, 3-5 mm wide at the base, 9-22 cm long, usually not exceeding the uppermost leaf-blades in length, angular, contorted, usually becoming caudate and lax toward the apex, the basal branches 6-13 cm long, 1-2.5 cm distant, the upper quarter of the rachis simple, the branches subhorizontal or often subdeflexed angular- or arcuate-ascending, the flowers fasciculate on a short sympodium or on compressed tertiary branches. *Flowers* with the pedicels 7-10 mm long, slender, ca 0.5 mm wide, swollen toward the apex,

granulose; bracts persistent, ovate, ca 1 mm long, acute, curled; sepals linear-ovate, 6-7.5 mm long, 2-2.8 mm wide; petals obovate-spatulate, 8.5-9 mm long, 6-7.5 mm wide, usually inequilateral and bilobed, rounded at the apex, subspatulate at the base; anthers 5-6 mm long; stipe of pistil ca 0.5 mm long, the ovary ca 1.2 mm long, the style subulate ca 5.5 mm long. *Fruits* with the pedicels bright red, curved, 6.5-8.5 mm long, ca 0.75 mm wide, the torus obovate-oblong to rotund, 5-10 mm long, the drupes oblong-rotund to subrotund, up to 9 mm long and 8 mm wide.

Known from Mexico, Guatemala, British Honduras, Honduras, Guatemala, and Panama.

PANAMA: Gatun, *Hayes 506* (NY).

Despite the fact that I accepted Riley's separation of *O. pyramidalis* Riley from *O. insulae* in my treatment of *Ouratea* in 1944 (Lloydia **7:** 137-138), I now feel that they are conspecific. The description is prepared from a wide range of material examined.

4. **Ouratea cocleensis** Dwyer, Phytologia **14:** 439, 1967.

Trees to 10 m high; branches terete, smooth, glabrous. *Leaves* with the petioles up to 0.8 cm long; blades oblong-rotund, up to 11 cm long, up to 4.5 cm wide, the narrower leaves tapering cuneately at the apex, the wider ones rounded at the apex, rounded or obtuse at the base, thinly coriaceous, smooth, shiny, glabrous, the costa plane above, prominent beneath, the lateral veins ca 15, prominulous but not evanescent, widely arcuate, with the intermediate veins few, irregular, the margins regular or somewhat repand, the teeth minute, ca 3-5 mm apart; stipules often persistent, amplexicaul, divergent, rectangular, up to 1 cm long, tapering narrowly and cuneately at the apex. *Inflorescences* axillary, pyramidal-paniculate, up to 12 cm long, up to 11 cm wide, the branches few, patulous, plano-compressed, somewhat contorted, the lowermost up to 6 cm long, the flowers solitary or paired on scarcely measureable tertiary branches, the articulation-stalks ca 1.5 mm long, the pedicels stiff, stout, ligneous, ca 1 cm long, expanding gradually and conspicuously toward the perianth. *Flowers* with the buds ovate to ovate-rotund, acute at the apex; petals ca 8 mm long. *Fruits* not seen.

Known only from the type locality.

COCLÉ: Cerro Pajita, N of El Valle de Antón, 3500 ft alt, *Allen 4497* (MO).

5. **Ouratea flexipedicellata** Dwyer, Phytologia **14:** 439, 1967.

Shrubs (?) with the branches terete, smooth. *Leaves* with the petioles up to 0.8 cm long, stout, ascending, well-spaced; blades narrowly oblong, up to 25 cm long, 6.5 cm wide, often widest slightly above the middle, gradually cuneate toward the apex, the ultimate acumination up to 1.2 cm long, obtuse at the base, thinly coriaceous, lustrous, glabrous, with the costa prominulous above, somewhat prominent below, the lateral veins ca 10, slender and somewhat prominulous above,

more conspicuous beneath, strongly arcuate, with the intermediate veins evanescent above, somewhat conspicuous beneath, occasionally not strongly arcuate and becoming evanescent toward the margin, with the margin somewhat thickened, scarcely repand, the teeth minute, 4-7 mm apart, serrate above, the teeth along the upper 1/3 of the margin divergent, up to 1 mm long. *Inflorescences* axillary or terminal, narrowly racemiform-paniculate, 8-30 cm long, with the rachises arcuate proximally, delicately flexuose distally, terete, up to 0.15 cm wide, minutely puberulent, the bostryces located almost to the base of the rachis, 3-5-flowered, those below the middle of the rachis well-spaced, 0.5-2 cm apart, the branches much reduced, 0.2-1 cm long; pedicels filiform, ca 0.75 mm wide in the middle, conspicuously reflexed, minutely puberulent, the articulation-stalks ca 1-2 mm long. *Flowers* with the buds (one seen) narrowly ovate, up to 0.9 cm long. *Fruits* (here immature) with the receptacle oblong, up to 8 mm long, the drupes elliptic-rotund, 4 mm long.

Known only from the type locality.

DARIEN: forest nr Pidiaque, *Duke 8050* (MO).

6. **Ouratea patelliformis** Dwyer, Phytologia **14:** 440, 1967.

Trees up to 6 m; branches terete, smooth, glabrous. *Leaves* well-spaced, with the petioles up to 0.8 cm long, somewhat thickened; blades narrowly elliptic, 15-20 cm long, 5-7 cm wide, cuneate toward the apex, acuminate and ultimately acute, obtuse or subcuneate at the base, thin-coriaceous, lustrous, smooth, glabrous, with the costa prominulous above, often plane toward the petiole, somewhat prominent beneath, the lateral veins ca 20, somewhat evanescent, widely arcuate, often the basal ones more sharply ascending, with the margins doubly serrate above the middle, or occasionally along the whole length, with the longer tooth more patulous. *Inflorescences* axillary or terminal, narrowly racemiform-paniculate, 11-18 cm long, the rachises slender, rubescent, ca 2 mm wide, twisted and plano-compressed, the branches few, 0.4-4.5 cm long, the bostryces solitary or paired, the lower and middle ones 3-5-flowered, the articulation-stalks up to 0.3 cm long, the pedicels ca 7 mm long. *Flowers* not seen. *Fruits* with the receptacle patelliform, ca 4 mm long, 6-10 mm wide, the scars of the druplets centrally located on the upper side of the torus, circular, ca 2 mm wide, obviously depressed.

Known only from type collection.

CANAL ZONE: Pacora, *Allen 3445* (MO).

7. **Ouratea lucens** (H.B.K.) Engler in Mart., Fl. Bras. **12**(2): 350, 1876.—Fig. 2.

Gomphia lucens H.B.K., Nov. Gen. Sp. Pl. **7:** 249, 1825.
Ouratea guatemalensis Engler in Mart., Fl. Bras. **12**(2): 345, 1876.
Gomphia nitida Helsl., Biol. Veg. Centr.-Amer. **1:** 176, 1879, non Sw., Fl. Ind. Occ. **2:** 739, 1800.
Stenouratea wrightii van Tieghem, Ann. Sci. Nat., Bot. sér. 8, **16:** 219, 1902.
Ouratea peckii Riley, Kew Bull. **1924:** 109, 1924.
O. stenobotrys Riley, loc cit.

O. isthmica Riley, loc. cit. 108.
O. wrightii (van Tieghem) Riley, loc. cit. 110.
O. podocarpa Sprague & Riley, loc. cit. 364.
O. lucens var. *podogyna* (J. D. Sm.) Williams, Fieldiana: Bot. **29**: 352, 1961.

Shrubs to small trees; branchlets terete, smooth, glabrous. *Leaves* with the petioles 0.5-1.2 cm long, lanceolate, rarely obovate, occasionally narrowly elliptic, 5.5-22 cm long, 2-7.5 cm wide, tapering deltoidly or acutely at the apex, usually short-acuminate, the acumen ultimately acute, cuneate to subobtuse at the base, the lamina thinly coriaceous or stiffly chartaceous, lustrous, smooth, glabrous, often drying gray-green above, the costa prominulous, the lateral veins delicately prominulous, usually somewhat evanescent, either very densely crowded and with little evidence of well-spaced veins dominating or with 10-12 more conspicuous and slender well-spaced veins, these at first widely arcuate then sharply ascending toward the margin, the intermediate veins crowded, the margin variable, serrulate, serrate or occasionally delicately repand along the upper ⅔, occasionally so to the base, the teeth either evanescent and reduced to glandular punctations, these often alternating large and small, or the teeth prominent, alternating large and small, either vaguely or distinctly uncinate, or rarely divergent and argute. *Inflorescences* racemiform, 2.5-14 cm long, 2-4 cm wide, the rachis slender, 1-1.5 mm wide, wiry and occasionally flexuous, erect or somewhat lax, glabrous, floriferous to the base or only along the upper ⅔, the flowers solitary or disposed in groups of 2-3 on reduced sympodia, 1-2 (-4) mm long, the pedicels slender, often filiform, up to 10 mm long, stiff and spreading, short-articulate at the base. *Flowers* with the buds ovate, acute; sepals 6-9 mm long; petals yellow, ca as long as the sepals. *Fruits* with the receptacles (4-) 6-13 mm long, obovate or compressed-ovate, occasionally almost twice as long as broad, often as broad as long, the druplets widely elliptic, up to 10 mm long, constricted at the base, the pedicels lignose and stiff.

Known from sporadic collections throughout Mexico and Central America.

BOCAS DEL TORO: Almirante, *Cooper 465* (NY); Chiriquí Lagoon, *von Wedel 1437* (MO), *1648* (MO); Old Bank I, *von Wedel 2031* (MO); Isla de Colón, *Woodson et al. 1948* (MO); s. loc., *von Wedel 314* (MO); CANAL ZONE: mouth of Río Chagres, *Allen 893* (MO); drowned forest of Quebrada Tranquilla, *Dodge & Allen 17330* (MO), *17502* (MO); Quebrada Ancha, *Dodge & Steyermark 17045* (MO); Albrook, *Dwyer & Robyns 46* (MO); Chagres, *Fendler 303* (MO); Gatun, *Hayes 12* (MO); Barro Colorado I, *Robyns 65-4* (MO), *Shattuck 243* (MO), *456* (MO); drowned forest of Quebrada below Río Indio Hydrographic Station, *Steyermark 17386* (MO); Quebrada Peluca & Río Boqueron, *Steyermark & Allen 17259* (MO); CHIRIQUÍ: San Felix, *Pittier 5190*. COCLÉ: Penonome, *Williams 223* (NY), *577* (NY); Bismark, *Williams 546* (NY). DARIEN: mouth of Río Lara, *Tyson & Loftin 3850* (MO); ridge NW of Yavisa, *Duke 6535* (MO); Cerro Pirre, *Duke 6551* (MO); Río Pirre, *Duke & Bristan 8298* (MO). HERRARA: 4 mi S of Los Pozos, *Tyson 2676* (MO). LOS SANTOS: Tonosi, *Mell s.n.* (NY); rd betw Tonosi & Llano de Piedras, *Stern et al. 1907* (MO); 11 mi N of Tonosi, *Tyson et al. 2982* (MO); 16 mi S of Macaracas at Quebrada Bejuco, *Tyson et al. 3089* (MO). PANAMA: Pacora, *Allen 3445* (MO); 7 mi N of Cerro Azul on rd to Cerro Jefe, *Blum et al. 1800* (MO); betw Capira & Potrero, *Dodge & Hunter 8649* (MO); Cerro Azul, *Dwyer 1371* (MO); Río Tocumen, N of Chepo Rd, *Hunter & Allen 220* (MO); San José I, M-area Rd, *Johnston 579* (MO).

After studying this species in the field as well as in the herbarium, I find it unusually polymorphic, particularly in terms of the character of the foliage and

Fig. 2. *Ouratea lucens* (H.B.K.) Engler: A, habit (×½); B, flower, long. sect. (×4); C, pistil (×5); D, stamen (×4); E, branch of inflorescence with fruiting receptacles and drupes (×1). A-D after *Dodge & Allen 17330* (MO); E after *Dwyer & Robyns 46* (MO).

the inflorescence. The leaf blades are quite variable in shape with the leaf margins showing a wide range of serration and serrulation. The inflorescences range from having the flowers solitary (and then the axis is often very short) to clusters of flowers on very reduced sympodia.

8. **Ouratea mexicana** (H. & B.) Engler in Mart., Fl. Bras. **12**(2): 312, 1876.

Gomphia mexicana H. & B., Pl. Aequin. **2:** 21, 1809.
Ouratella mexicana van Tieghem, Ann. Sci. Nat., Bot. sér. 8, **16:** 219, 1902.
Ouratea pallida Standley, Contr. U.S. Nat. Herb. **23:** 820, 1923.

Shrubs, small; branches drying ashen-gray smooth but often gnarled, the branchlets arising almost at right angles, soon defoliated, short, stiff and spike-like; stipules deciduous. *Leaves* shortly petiolate, clustered at the apices of the branches, soon deciduous; blades somewhat narrow-elliptic, elliptic-obovate, oval-elliptic or ovate, 4-9 cm long, 2-3 cm wide, rounded or widely cuneate at the apex, obtuse to cuneate at the base, coriaceous, lustrous, the costa prominulous above and below, the lateral veins ca 15, prominulous, somewhat evanescent, arcuate-ascending, the intervenal areas patulous, prominulous, the margin delicately repand or vaguely serrulate, the teeth disposed as glandular points. *Inflorescences* racemiform (or paniculate?), shorter than the leaves (or longer fide Standley), the rachis slender, stiff, the flowers usually in relatively dense clusters, with 3 flowers per cluster, on very reduced sympodia up to 2 mm long, the pedicels ca 8 mm long, slender. *Flowers* appearing before the leaves; buds ovate, ca 5 mm long; sepals 5-7 mm long; petals up to 9 mm long. *Fruits* with druplets up to 1 cm long, very lustrous and black.

Known from Mexico and Panama.

COCLÉ: Penonome, *Williams* 353 (NY).

3. SAUVAGESIA

Sauvagesia L., Sp. Pl. 203, 1753.

Sauvagea Neck., Elem. Bot. **2:** 378, 1790.
Roraimanthus Gleason, Phytologia **1:** 39, 1933.

Herbs or rarely low shrubs, glabrous; stems usually branched; roots fibrous. *Leaves* subsessile, the blades with the costa usually prominent above and below, the margin ciliate, the lateral veins sharply ascending; stipules persistent, ciliate. *Inflorescences* with the bostryces either axillary and fasciculate or terminal and paniculate, rarely solitary. *Flowers* pedicellate; sepals 5, quincuncial, subequal, expanded at anthesis, appressed and persistent in the fruit; petals 5, imbricate in the bud, deciduous; segments of the exterior corona present or absent, usually filamentous, shorter than the interior corona, disposed in 1-3 continuous whorls, or fasciculate and opposite the stamens, persistent in the fruit; segments of the interior corona 5, free, petaloid; stamens 5, the filaments often longer than the anthers; ovary flask-shaped, 3-carpellate, the placentae parietal, the ovules ∞, the style longer than the ovary, occasionally persistent in the unopened fruit. *Capsules* smooth, acute, the seeds round, reticulate, not winged.

Widely distributed throughout the tropics of the New World. *Sauvagesia erecta* may be native to Africa.

a. Stipules with cilia bearing an obvious gland .....1. *S. pulchella*

aa. Stipules with eglandular cilia.

b. Herbs up to or exceeding 10 cm; exterior corona present.

c. Bostryces axillary; herbs up to 0.5 dm; median leaves up to 1.3 cm wide .....2. *S. erecta*

cc. Bostryces terminal; herbs up to 10 dm; median leaves 1.5-2.5 cm wide .....3. *S. elata*

bb. Herbs up to 3-7 cm; exterior corona absent .....4. *S. tenella*

1. **Sauvagesia pulchella** Seem., Bot. Voy. Herald 80, 1853.

Herbs 5-15 cm long; branches short, arising near the middle of the stem. *Leaves* subsessile, elliptic, ca 17 mm long, 2-4 mm wide, acute at the apex, cuneate at the base, the lamina scarcely alate on the petiole, the lateral veins prominent; stipules linear or elliptic, curved, up to 6 mm long, the cilia elongate, each cilium with a median and laterally disposed gland. *Inflorescences* with the bostryces 2-5-flowered, crowded in the axils of the uppermost leaves; pedicels up to 5 mm long, the articulation-stalks ca 1 mm long; bracts linear or lanceolate, the margins serrate, ciliate basally, the cilia not glandular-jointed. *Flowers* with the sepals lanceolate, 1.5-1.7 mm long, acute, the margins entire and bearing a few short cilia toward the apex, often with a distinct terminal cilium, the veins ca 3; petals elliptic, ca 1.8 mm long, rounded at the apex, the veins ca 3; exterior corona absent; segments of the interior corona oblong, ca 1.5 mm long, the veins several, the median vein more conspicuous and branching; anthers subrotund or ovate, ca 0.4 mm long, obtuse to acuminate at the apex, the filaments ca 0.5 mm long; ovaries ovate, up to 1.5 mm long, the style ca 0.5 mm long. *Fruits* ovate, ca twice the length of the sepals.

Known from Panama and N South America.

COCLÉ: El Valle de Antón, *Allen 1151* (MO). PANAMA: betw Pacora & Chepo, *Dodge et al. 16697* (MO).

2. **Sauvagesia erecta** L., Sp. Pl. 203, 1753.—Fig. 3.

S. adima Aubl., Hist. Pl. Gui. Fr. 251, 1775.
S. nutans Pers., Syn. Pl. **1:** 253, 1805.
S. peruviana Roem. & Schult. in L., Syst. Veg. ed. nov., **5:** 437, 1819.

Herbs, woody, rarely subshrubs, simple or branched. *Leaves* with the petioles up to 0.5 cm long; blades oblong-lanceolate, 1.2-6 cm long, 0.3-1.2 cm wide, acute at the apex, cuneate at the base, membranaceous, glabrous, the costa prominent, the lateral veins prominent above, 1-1.5 mm distant, spreading from the costa at a 30° angle; stipules linear-subulate, up to 5.5 mm long, the cilia elongate, up to 6.5 mm long. *Inflorescences* axillary, the flowers 1-3 per bostryx, the pedicels deflected, slender, up to 2 cm long. *Flowers* with the sepals lanceolate, 3.8-6 mm long, obtuse at the apex, clawed at the base; segments of the exterior corona numerous, in 1-3 continuous whorls, rotund- to reniform-capitate, the filaments 1-2 mm long, up to ½ the length of the segments of the interior corona, the innermost the longest; segments of the interior corona obovate-oblong, 3-5 mm long, rounded

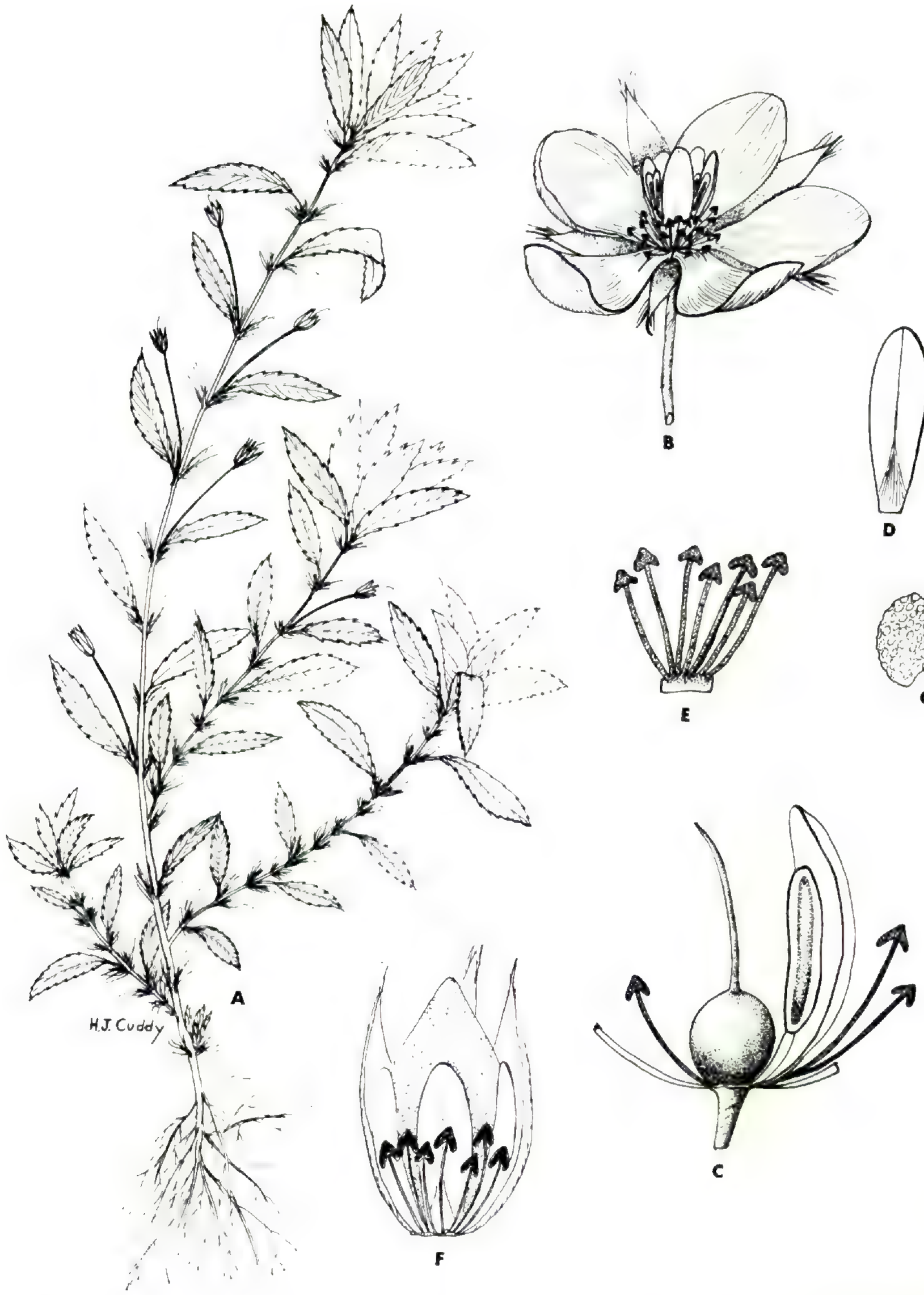

Fig. 3. *Sauvagesia erecta* L.: A, habit (×½); B, flower (×3); C, gynoecium, one stamen, one segment of the interior corona, and three filaments of the outer corona, sepals and petals removed, adaxial view (×½); D, segment of interior corona, adaxial view (×10); E, segment of exterior corona, adaxial view (×10); F, fruit with exterior and interior coronal segments, and three sepals shown, adaxial view (×10); G, seed (×1). A-G after *Ebinger 1142* (MO).

or truncate at the apex, tapering toward the base, the median ridge conspicuous and expanded at the base; anthers oblong or linear-oblong, usually 2-2.5 mm long, up to 4/5 the length of the interior corona; ovary subrotund, up to 1.5 mm long, the style up to 3.5 mm long. *Fruits* often exceeding the sepals in length, 3.5-7 mm long.

A pantropic weed.

BOCAS DEL TORO: Bocas, *Cooper 465* (F); Old Bank I, *von Wedel 2029* (MO, NY); SW Bocas at Macaw Hills, *von Wedel 524* (MO). CANAL ZONE: first bridge N of Miraflores on Gaillard Hwy, *Blum 458* (MO); Río Azote Caballo, *Dodge et al. 16832* (MO), *16852* (MO); Chagres, *Fendler 102* (MO); Farfan Beach, *Lewis et al. 329* (MO); Ancon Hill, *Piper 5579* (NY); Fort Sherman on Pina Rd, *Tyson & Chu 1707a* (MO). CHIRIQUÍ: Boquete, *Davidson 569* (MO), *Woodson & Schery 786* (MO); betw Boquete & David, *McDaniel 6796* (MO). COCLÉ: El Valle de Antón, *Allen 1164* (MO), *2576* (MO); Nata, *Allen 8330* (MO); betw Las Margaritas & El Valle de Antón, *Woodson et al. 1259* (MO). COLÓN: Portobello, *Ebinger 1142* (MO). PANAMA: Panama Viejo, *Duke 5732* (MO), *5747* (MO); Cerro Campana, *Duke 8684* (MO), *Ebinger 929* (MO); San José, I, East Bay, *Johnston 190* (MO); rd to Cerro Jefe, 2-3 mi S of Goofy Lake, alt 2000-2200 ft, *Lewis et al. 234* (MO); Cerro Azul, *Tyson 2045* (MO).

3. **Sauvagesia elata** Benth. in Hook., Lond. Jour. Bot. **4:** 107, 1845.

Herbs, woody or shrubby, up to 1 m. *Leaves* with the petioles 3-5 mm long; blades lanceolate, the middle ones usually 6-12 cm long, 1.5-2.5 cm wide, acuminate at the apex, glabrous, chartaceous, shiny above, the margin delicately thickened, undulate, the teeth minute, well-spaced, the costa slender, prominulous, the lateral veins slender, crowded, arcuate-ascending; stipules appressed or spreading, the corpus linear or narrowly deltoid, 1-1.5 cm long, striate, the marginal cilia longer than the body, the cilia curled and arachnoid. *Inflorescences* with the bostryces fasciculate and terminal, extending 6-10 cm beyond the uppermost leaves; pedicels slender, up to 6.5 mm long, the articulation-stalk 1.5-2 mm long. *Flowers* with the sepals lanceolate to ovate-lanceolate, ca 6 mm long, acute, with a solitary glandular cilium at the apex, this rarely subtended by glandular teeth; petals white, oblong, as long as or shorter than the sepals, retuse at the apex, the notch with 1-3 glandular cilia; segments of the exterior corona filamentous, scarcely swollen at the apex, in 1-3 continuous whorls, the innermost whorl up to 2/5 the length of the interior corona; segments of the interior corona obovate or oblong, up to 4 mm long, the median ridge conspicuous, the veins prominent and flabellate; stamens oblong or almost subulate, ca 2/5 the length of the interior corona, the filaments short; ovary ovate or flask-shaped, the style short, crassate, constricted basally, slightly longer than the ovary. *Fruits* subrotund, equal to or exceeding the sepals in length.

Known only from Panama and British Guiana.

BOCAS DEL TORO: Old Bank I, Chiriquí Lagoon, *von Wedel 2029* (MO).

4. **Sauvagesia tenella** Lam., Encycl. Méth. Bot. **2:** 119, 1797.

S. nana Ule, Notizbl. Bot. Gart. Berlin **6:** 345, 1915.
S. gracilis Ule, loc. cit.
S. inconspicua Dwyer, Lloydia **2:** 195, 1939.

Herbs 0.3-0.7 dm tall; branches absent or occasionally few at the apex or base, glandular, smooth. *Leaves* sessile, elliptic, 3-8 mm long, 1.8-3 mm wide, subacute or obtuse at the apex, subcuneate at the base, delicately carnose, the margin entire or depressed-serrate above the middle, the tips of the cilia minutely falcate-dentoid the lateral veins evanescent; stipules linear or oblong, 1-3 mm long, the cilia well-spaced and exceeding the corpus in length. *Inflorescences* with the bostryces terminal, solitary or rarely paired; bracts stipuloid, minute; pedicels slender, 6-7 mm long. *Flowers* with the sepals lanceolate to ovate, 3.2-4 mm long, setose-aristate at the apex, the margins usually scarious, the veins ca 3; petals pink, white or yellow, obovate, 3-5 mm long, equal to or exceeding the sepals in length, usually unguiculate at the base, the veins evanescent; segments of the exterior corona absent; segments of the interior corona usually oblong, rarely narrowly obovate, usually slightly shorter than the stamens, rounded or obtuse, the median vein evanescent, the dorsal furrow absent, the veins 1-2, ascending; stamens up to 2 mm long, the anthers oblong, obtuse, often longer than the filaments; ovary ellipsoid or rotund, ca 1 mm long, exceeding the style in length. *Fruit* equal to or exceeding the sepals in length, mostly turgid at the base.

Cuba, Central America and tropical South America.

CHIRIQUÍ: David Airport, *Lewis et al. 745* (MO). COCLÉ: betw Las Margaritas & El Valle de Antón, *Woodson et al. 1233* (MO); s. loc., *Allen 830* (NY). PANAMA: San José, *Erlanson 587* (NY); betw Pacora & Chepo, *Woodson et al. 1657* (MO, NY).

Excluded Material

One of my recent collections (*7082*) from Cerro Azul, 8 mi S toward Cerro Jefe, Province of Panama, superficially resembles *Ouratea lucens* (H.B.K.) Engler but its narrowly salicoid leaves, up to 2.5 cm wide, and its contracted panicle with a thin wiry rachis and branches are not typical of the species. I shall defer judgment on this.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 122. THEACEAE[1]

BY ANDRÉ ROBYNS[2, 3]

Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Shrubs or small to large trees. *Leaves* usually alternate, estipulate, simple, often ± coriaceous, the margins entire to serrate, persistent or not. *Flowers* axillary, solitary or fasciculate, rarely in axillary or terminal racemes, usually ☿, actinomorphic, usually 2-bracteolate; sepals 4-7, free or mostly ± connate at the base, imbricate, often persistent; petals 5, rarely 4-many, imbricate, alterni- or sometimes episepalous, free or connate into a short ring at the base; stamens 5 or 10 or mostly numerous, uni- or many-seriate, free or often united basally, often adnate to the base of the petals, the anthers basifixed or versatile, 2-thecate, longitudinally dehiscent; pollen grains with the exine nearly smooth to finely reticulate; ovary superior, rarely half-inferior or inferior, syncarpous, (1-)2-10-celled, mostly 3- or 5-celled; the ovules (1-)2-∞ per cell, axile, pendulous or erect; styles isomerous with the cells of the ovary, distinct or united into one, rarely absent. *Fruits* capsular, loculicidally dehiscent, with the central columella persistent, and with a ligneous or, less frequently, coriaceous pericarp (*Camellioideae*), or baccate or rarely pomelike, with the pericarp fleshy, coriaceous, or dry (*Ternstroemioideae*); seeds 1-∞, small to fairly large, alate or not; endosperm copious or absent; embryo slender to broad, straight or curved or hippocrepiform.

A family of about 30 genera and over 350 species distributed mainly in tropical and subtropical regions of both hemispheres, but not well represented in Africa, and with a few genera and species extending into temperate regions; six genera and seven species, at present, reported from Panama.

Camellia sinensis (L.) Kuntze, the tea plant, native to China and India, is the most important economic plant of the family; the genus *Camellia* L. and some other genera contribute significant ornamentals from warm climates.

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2] Visiting Curator of the Flora of Panama, Missouri Botanical Garden; *Chargé de Recherche* of the National Foundation for Scientific Research, Belgium.

[3] I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and for the loan of material: Field Museum of Natural History (F), New York Botanical Garden (NY), and U. S. National Herbarium (US).

ANN. MISSOURI BOT. GARD. **54**(1): 41-56, 1967.

The following publications were found helpful in preparing this manuscript:

Keng, H. Comparative morphological studies in *Theaceae.* Univ. Calif. Publ. Bot. **33:** 269-384, 7 *pl.*, 30 *figs.*, 1962.

Melchior, H. *Theaceae* in Engler & Prantl, Nat. Pflanzenfam. ed. 2, **21:** 109-154, *fig.* 59-67, 1925.

a. Anthers versatile; fruit capsular .....1. *Laplacea*
aa. Anthers basifixed; fruit indehiscent.
  b. Stamens 5; sepals caducous; flowers large; mangroves .....2. *Pelliciera*
  bb. Stamens more than 5; sepals persistent; flowers small.
    c. Leaves densely appressed-sericeous beneath; anthers glabrous .....3. *Freziera*
    cc. Leaves glabrous or glabrate, at least in age.
      d. Ovary inferior; anthers glabrous .....4. *Symplococarpon*
      dd. Ovary superior.
        e. Anthers setose; petals alternisepalous .....5. *Cleyera*
        ee. Anthers glabrous; petals episepalous .....6. *Ternstroemia*

1. LAPLACEA

Laplacea H.B.K., Nov. Gen. Sp. Pl. **5:** 161, *t. 461*, 1822, nom. gen. conserv.

Wikstroemia Schrader, Götting. Gel. Anzeig. **1821**(71): 710, 1821.

Trees or shrubs. *Leaves* alternate, the blade symmetrical or asymmetrical, membranous to coriaceous, the margins dentate to entire. *Flowers* mostly solitary in the axils of the uppermost leaves, ☿, pedicellate, 2-3-bracteolate, the bracteoles sepaloid and caducous; sepals usually 5, unequal, coriaceous, caducous or persistent; petals usually 5, unequal, connate basally, deeply cleft at the apex or not; stamens ∞, many-seriate, the filaments usually adnate to the base of the petals, sometimes connate at the base or throughout and forming a staminal tube free from the petals, the anthers versatile, glabrous; ovary superior, (4-)5(-6-10)-celled, the ovules 4-many in each cell, with as many divergent styles as cells in the ovary or with the stigmas sessile or nearly so. *Capsules* ± ligneous, loculicidally dehiscent nearly to the base, the columella persistent; seeds numerous, flat or compressed, alate; endosperm none or scant; embryo straight; cotyledons thick and fleshy.

A neotropical genus of eight species; two species, at present, reported from Panama.

Useful reference:

Kobuski, C. E. Studies in the *Theaceae,* XX. Notes on the South and Central American species of *Laplacea.* Jour. Arnold Arb. **31:** 405-429, 1950.

a. Leaf blades markedly asymmetrical; sepals deciduous .....1. *L. fruticosa*
aa. Leaf blades symmetrical; sepals persistent .....2. *L. grandis*

1. **Laplacea fruticosa** (Schrader) Kobuski, Jour. Arnold Arb. **28:** 437, 1947.— Fig. 1.

Wikstroemia fruticosa Schrader, Götting. Gel. Anzeig. **1821**(71): 711, 1821 (as *fructicosa*).
Laplacea semiserrata (Mart. & Zucc.) Camb. in St.-Hil. *et al.*, Fl. Bras. Merid. **1:** 300, 1827.

Tree to 30 m high, the trunk to 75 cm in diam, the branchlets appressed-pubescent to glabrous. *Leaves* grouped towards the apex of the branchlets, sessile to subsessile; blade markedly asymmetrical, to 8 cm long, the smaller side as half of a narrow ellipse and 1 cm or less wide, the larger side usually wider above the middle and to 1.8 cm wide, long-attenuate and decurrent at the base, obtuse and

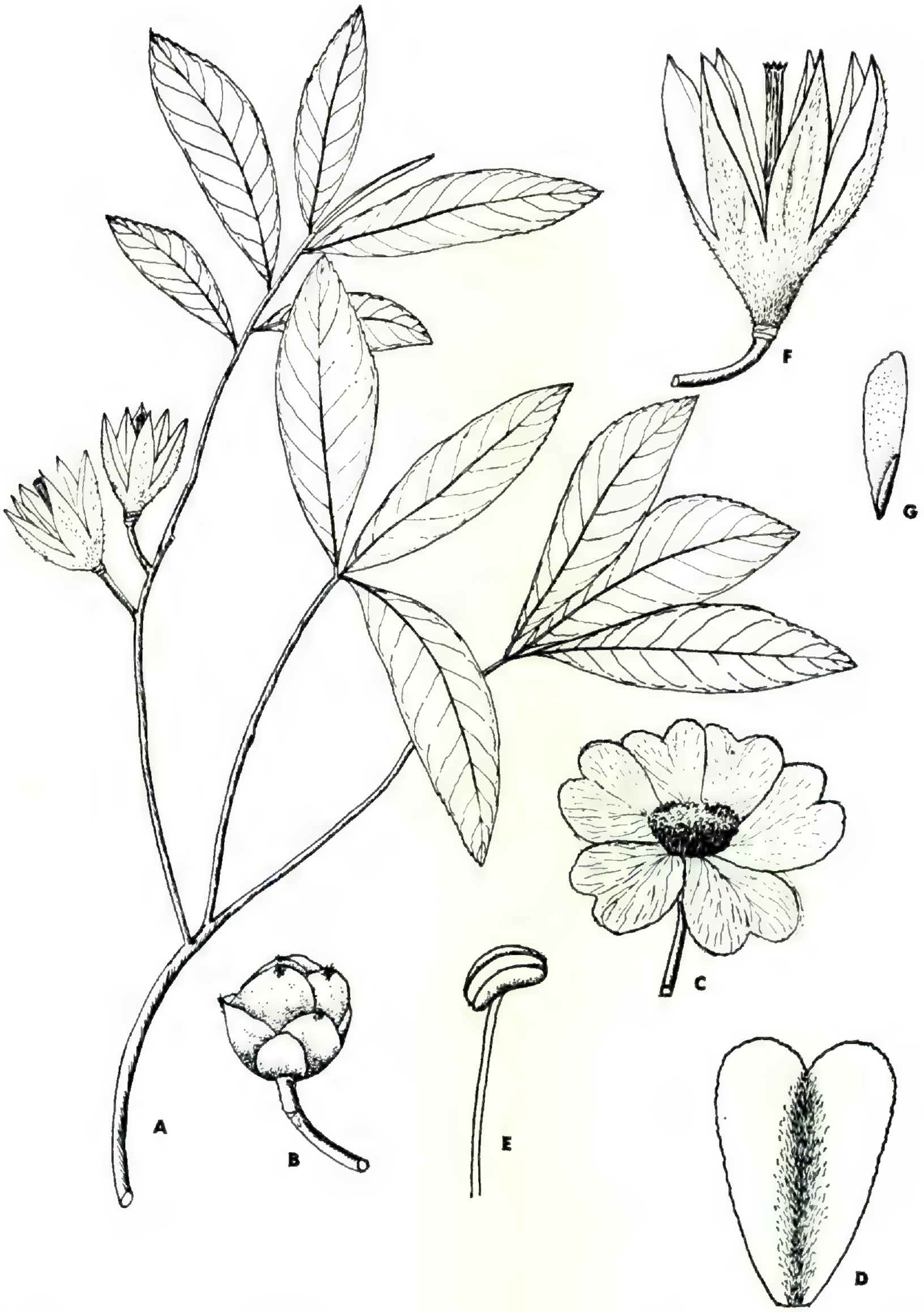

Fig. 1. *Laplacea fruticosa* (Schrader) Kobuski: A, habit (×½); B, flower bud (×1); C, flower (×½); D, petal, dorsal view (×1); E, stamen with versatile anther (×10); F, dehiscent capsule (×1½); G, seed (×1½). A, F & G after *Little 6061* (F); B-E after *Allen 2085* (MO).

mostly subretuse at the apex, rigid-chartaceous to subcoriaceous, the margin entire along the narrower side, serrulate, sometimes obscurely so, along the upper part of the wider side, glabrous or appressed-puberulous especially along the midvein on the lower surface, the midvein slightly impressed above and prominent below, the lateral veins ± inconspicuous on both sides. *Flowers* axillary, solitary, shortly pedicellate, the pedicel to 1 cm long, to 1.5 cm long in fruit, terete, glabrous or appressed-puberulous; bracteoles 2, large, inserted immediately beneath the calyx, subcircular; sepals 5, subcircular, to 1 cm long, appressed-puberulous dorsally except for the membranous margins, or only at the apex, caducous; petals white, 5-7, obovate, deeply cleft at the apex, to 3 cm long and 2 cm wide, puberulous medially without; stamens ca ¼-½ the length of the petals, the filaments connate at the base; ovary globose, densely sericeous when young, ridged, 5-7-celled, each cell with few ovules; styles 5-7, short, the stigmas subbifid and spreading. *Capsules* obovoid, to 2.5 cm long, glabrescent, 5-7-valvate; seeds to 12 mm long (wing included), the wing to 4 mm wide.

A polymorphic species distributed in Honduras, Costa Rica, Panama, and tropical South America; known locally as *mangle de monte* (cf. *Stern & Chambers 46*).

CHIRIQUÍ: nr sawmill on Río Chiriquí Viejo, 3 km N of Camp El Volcán, alt 4300 ft, rain forest, *Little 6061* (F, MO, US); foothills of Volcán Barú, N of El Hato, alt 5000 ft, *Stern & Chambers 46* (F, MO, NY, US); Río Indio drainage, ca 9 mi E of Trans-Isthmian Hwy, alt 800 ft, medium slope, clay loam soil, rain forest, *Barbour 1055* (F).

2. **Laplacea grandis** Brandegee, Univ. Calif. Publ. Bot. **6:** 186, 1915.

Tree up to 24 m high, the trunk to 80 cm in diam; branchlets terete, minutely stellate-puberulous when young, glabrescent. *Leaves* grouped towards the apex of the branchlets, shortly petiolate, the petiole minutely stellate-puberulous; blade symmetrical, elliptic, tapering toward the base and decurrent, acute at the apex, to 13 cm long and 4.5 cm wide, coriaceous, the margin crenate-serrate, minutely stellate-puberulous especially on the lower surface, becoming glabrescent in age, the midvein prominent beneath, the lateral veins conspicuous but complanate on both surfaces. *Flowers* solitary in the axils of the uppermost leaves, the pedicels terete, to 3 cm long, densely and minutely stellate-puberulous to minutely stellate-tomentellous, the bracteoles 2-3, narrowly oblong-ovate, acute, to 6 mm long and 2.5 mm wide, minutely stellate-tomentellous; sepals 5, depressed-ovate, rounded, 2-3 mm long and 4-5 mm wide, minutely stellate-tomentellous, conspicuously ciliolate along the margin, persistent; petals white, obovate, rounded, 1.5-2 cm long and 0.8-1.2 cm wide, connate basally into a tube 5 mm long, the outermost petal thicker and to 2 cm wide, stellate-puberulent dorsally, the other petals stellate-puberulent basally or medially outside; stamens 6-7 mm long, the filaments connate throughout or nearly so, the anthers oblong, ca 1.5 mm long; ovary oblong-ellipsoid, densely sericeous especially towards the base, 5-celled; stigmas 5, nearly sessile. *Capsules* oblong-ellipsoid, 2-3 cm long and 1-1.5 cm in diam, minutely and sparsely stellate-puberulous, 5-valvate; seeds 1-1.5 cm long (wing included), the wing 4-5 mm wide.

Mexico, Honduras, Costa Rica, and Panama.

PANAMA: Río Indio drainage, ca 9 mi from Trans-Isthmian Hwy, alt 800 ft, medium slope, clay loam soil, rain forest, *Barbour 1053* (F).

As the above Panamanian collection has only leaves and flower buds, the description of petals, androecium and gynoecium is based on the description given by Kobuski in 1950 (loc. cit. 416-417).

2. PELLICIERA

Pelliciera Triana & Planchon in Benth. & Hook., Gen. Pl. **1:** 186, 1862.

Trees, the trunk buttressed at the base. *Leaves* alternate, grouped towards the apex of the branchlets, sessile, the blade asymmetrical. *Flowers* large, axillary (apparently terminal), solitary, ☿, subtended by large foliaceous bracts; sepals 5, distinct, unequal, deciduous; petals 5, alternisepalous, free, much longer than the sepals, equal or subequal, caducous; stamens 5, alternipetalous, the filaments filiform, closely appressed within every other one of the longitudinal grooves of the ovary for most of their length, the anthers basifixed, long, subequal, 2-thecate, glabrous, the connective narrow and projecting into a mucro; gynoecium narrowly conical, divided almost equally into a longitudinal 10-sulcate ovary and a smooth style, the ovary superior, 2-celled, occasionally 1-celled by abortion, each cell with 1 large campylotropous ovule; stigmas punctate. *Fruits* indehiscent, coriaceous-fungose, 1-celled, 1-seeded; seed consisting of only 2 large fleshy obcordate cotyledons, a firm pointed radicle, and a large curved plumule; endosperm lacking.

A monotypic genus distributed in mangrove swamps along the Pacific coast of Nicaragua, Costa Rica, Panama, Colombia, and NW Ecuador.

Useful references:

Howe, M. A. A little-known mangrove of Panama. Jour. N. Y. Bot. Gard. **12:** 61-72, *fig. 16-23*, 1911.

Kobuski, C. E. Studies in the *Theaceae*, XXIII. The genus *Pelliciera*. Jour. Arnold Arb. **32:** 256-262, 1951.

1. **Pelliciera rhizophorae** Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **17:** 381, 1862.—Fig. 2.

Tree, sometimes shrubby, 3-15 m tall, glabrous, the crown elongate, the bark grey and lenticellate. *Leaves* with the blade narrowly elliptic, or narrowly ovate-elliptic, or narrowly obovate-elliptic, the apex acute to obtuse, to 15 cm long and 5 cm wide, coriaceous, the margin entire along the smaller side of the blade, often glandular-serrate along the upper half of the wider side of the blade when young, dark green, smooth, glabrous, the venation inconspicuous except the slightly prominent midrib on the lower surface. *Flowers* sessile, the buds linear, enveloped by the 2 bracts, these to 7 cm long and 2 cm wide, rose-colored to crimson; sepals oblong-elliptic to obovate, acute, strongly concave, thickened by glandular punctations in the middle, the margins membranous and entire, 1.5-2 cm long and 0.8-1.2 cm wide, crimson; petals usually white, occasionally pink, narrowly ovate, obtuse

Fig. 2. *Pelliciera rhizophorae* Triana & Planchon: A, habit (×½); B, bract (×½); C, sepal (×½); D, petal (×½); E, androecium and gynoecium (×1); F, fruit (×½). A after *Woodson et al.* 762 (MO); B-E after *Tyson et al.* 4678 (MO); F after *Stern & Chambers* 26 (MO).

to subacute, up to 7 cm long and 1.5 cm wide, membranous-hyaline except the thickened median portion; stamens with the filaments up to 3.5 cm long, the anthers linear, sagittate at the base, up to 3 cm long; gynoecium up to 6.5-7 cm long, the ovary ca 5 mm in diam. *Fruits* napiform, irregularly many-sulcate, abruptly long-beaked, 7-10 cm long (beak included), ca 8 cm broad and 2-3 cm thick, at first greenish-brown, later reddish-brown, the beak ⅓-½ of the total length; seeds with the cotyledons up to 6 cm long and 7 cm wide.

The ecology, dispersal and germination of this species are described in detail by Howe (loc. cit.).

Known locally as *palo de sal*.

CANAL ZONE: on banks of Río Grande, growing in mud, *Woodson et al.* 762 (MO, NY); betw Corozal & Ancon, alt 10-30 m, *Pittier* 2644 (NY); Balboa, on mud of estuary forming Pacific terminus of Panama Canal, with *Rhizophora, Avicennia, Laguncularia,* etc., *Howe s.n.* (NY); mud flats along coast nr Farfan, *Stern & Chambers* 26 (MO, US), *154* (MO); betw Farfan Beach & Palo Seco, alt 5 m, *Hunter & Allen* 445 (NY). DARIEN: 3 mi E of Sante Fé, pineapple mangrove, *Tyson et al.* 4678 (MO); along Río Tuira, 5-15 mi downstream from El Real, *Duke* 4946 (MO). PANAMA: Punta Paitilla, *Bro. Heriberto* 210 (US); Río La Maestra, alt 0-25 m, mangrove swamps, *Allen* 32 (F, MO); Río Pita, 0.2 mi above tidal limit, *Duke* 4792 (MO); San José I, mangrove swamp nr main beach, *Erlanson* 329 (US), *Johnston* 337 (MO).

3. FREZIERA

Freziera Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **2:** 1179, 1799 (vel Jan. 1800), nom. gen. conserv.

Eroteum Sw., Nov. Gen. Sp. Pl. Prodr. 5, 85, 1788.
Lettsomia Ruiz & Pavon, Fl. Peruv. Chil. Prodr. 77, 1794.

Trees or rarely shrubs. *Leaves* alternate, petiolate, usually coriaceous, glabrous to sericeous beneath, the margins usually serrulate, sometimes entire or nearly so. *Flowers* fasciculate in the leaf axils or on abbreviated branchlets, sometimes axillary and solitary, dioecious or polygamous, 2-bracteolate, the bracteoles opposite, inserted immediately beneath the calyx; sepals 5, unequal, persistent; petals 5, alternisepalous, unequal, usually distinct; stamens 15-30 in staminate or ☿ flowers, uniseriate, the filaments adnate to the base of the corolla, the anthers basifixed, shorter than the filaments, glabrous; staminodes many in pistillate flowers; ovary superior, 2-5-celled, the ovules ∞ in each cell, the style entire, the stigma with the same number of lobes as cells in the ovary. *Fruits* indehiscent, dry; seeds ∞, small, reniform; endosperm fleshy; embryo nearly straight or slightly curved.

A neotropical genus of about 30-35 species; only one species reported from Panama.

Useful reference:

Kobuski, C. E. Studies in the *Theaceae,* VIII. A synopsis of the genus *Freziera.* Jour. Arnold Arb. **22:** 457-496, 1941.

1. **Freziera candicans** Tulasne, Ann. Sci. Nat., Bot., sér. 3, **8:** 328, 1847.—Fig. 3.

Eurya seemanniana Pittier, Contr. U. S. Nat. Herb. **20:** 480, 1922.
Freziera seemanniana (Pittier) Kobuski, Ann. Missouri Bot. Gard. **25:** 355, 1938.

Tree, sometimes shrub, 5-18 m high, the trunk to 35 cm in diam, the branchlets densely appressed-sericeous when young. *Leaves* long-petiolate, the petiole to 1.8 cm long, markedly canaliculate above, glabrous above, appressed-sericeous beneath; blade narrowly ovate to ovate or narrowly elliptic to elliptic, long-attenuate to acute and narrowly decurrent at the base, ± long-acuminate at the apex, to 13 cm long and 5.5 cm wide, rigid-chartaceous, discolor, the margins entire to subserrulate, glabrous above, densely lustrous-appressed-sericeous beneath, the midvein prominent beneath, the lateral veins numerous and prominulous on both surfaces. *Flowers* axillary, in fascicles of 3-7, polygamous, the pedicels to 8 mm long, ap-

Fig. 3. *Freziera candicans* Tulasne: A, habit (×½); B, flower (×4); C, id., longitudinal section (×5); D, stamen (×10); E, ovary, cross-section (×8); F, fruit (×3). A, F after *Woodson et al. 904* (MO); B-E after *Davidson* 562 (MO).

pressed-sericeous, the bracteoles sepaloid, subcircular, ca 2-3 mm long, sericeous; sepals concave, subcircular to broadly ovate, acute, to 5 mm long, sericeous outside; petals white or yellowish-white, broadly-ovate, rounded to ± cuneate, to 8 mm long and 5 mm wide, glabrous; stamens unequal in length, the filaments to 2.5 mm long, the anthers ca 1 mm long, minutely mucronulate at the apex; ovary ovoid, glabrous, 3-5-celled, the stigmas 3-5, spreading. *Fruits* globose, to 7 mm in diam, dark brown, 3-5-celled, many-seeded.

A polymorphic species distributed in Costa Rica, Panama, Colombia and Venezuela; the pubescence of the lower surface of the leaves when dry is yellowish-beige to beige; locally known as *sajinillo* (cf. *Pittier 2944*).

CHIRIQUÍ: vic of Callejón Seco, Volcán de Chiriquí, alt 1700 m, *Woodson & Schery 489* (MO, US); vic of Casita Alta, Volcán de Chiriquí, alt ca 1500-2000 m, *Woodson et al. 904* (F, MO, NY); Finca Lérida to Peña Blanca, alt 1750-2000 m, *Woodson & Schery 316* (MO, US); forested ridges S of Finca Lérida, alt 6000-7000 ft, *Allen 4756* (MO, NY, US); Chiquero, Boquete Distr, alt 6000 ft, *Davidson 562* (F, MO, US); forest around El Boquete, alt 1000-1300 m, *Pittier 2944* (type *F. seemannianna,* F, US); Boquete, *Dwyer 6952* (MO).

4. SYMPLOCOCARPON

Symplococarpon Airy-Shaw, Hook. Icon. Pl. **34:** *t.* 3342, 1937.

Trees. Leaves alternate, the blade ± coriaceous, the margins entire or serrate. *Flowers* axillary, fasciculate, ☿, pedicellate, 2-bracteolate, the bracteoles persistent; sepals 5, perigynous, persistent; petals 5, alternisepalous, perigynous, slightly connate basally; stamens 22-40, 1-seriate, the filaments adnate to the base of the corolla, the anthers basifixed, glabrous, mucronate at the apex; ovary inferior, the upper part slightly exerted above the base of the persistent calyx and glabrous or hirsute, 2-celled, each cell 1-2-ovulate; styles 2-3, usually distinct, the stigmas punctiform. *Fruits* indehiscent, almost dry, crowned by the persistent calyx and styles, 2-3-celled.

A genus of seven species; three species in Mexico, one in British Honduras, two in Costa Rica, and one in Panama.

Useful reference:

Kobuski, C. E. Studies in the *Theaceae,* VI. The genus *Symplococarpon* Airy-Shaw. Jour. Arnold Arb. **22:** 188-196, 1941.

1. **Symplococarpon chiriquense** Kobuski, Jour. Arnold Arb. **22:** 192, 1941.—Fig. 4.

Trees 6-9 m high, the branchlets glabrous. *Leaves* glabrous, the petiole 2-4 mm long; blade elliptic-obovate, attenuate-cuneate at the base, rounded-obtuse and subretuse at the apex, to 6 cm long and 3 cm wide, subcoriaceous, the margins entire, slightly lustrous above, dull below, the midvein complanate above and prominent below, the lateral veins prominulous on both sides. *Flowers* 3-4-fasciculate; pedicels filiform, recurved at the apex, to 12 mm long, the bracteoles subopposite, inserted near the apex of the pedicel, unequal, ca 0.5 mm long, ciliolate; sepals depressed-ovate, rounded, ca 1-1.5 mm long and 2 mm wide, ciliolate at

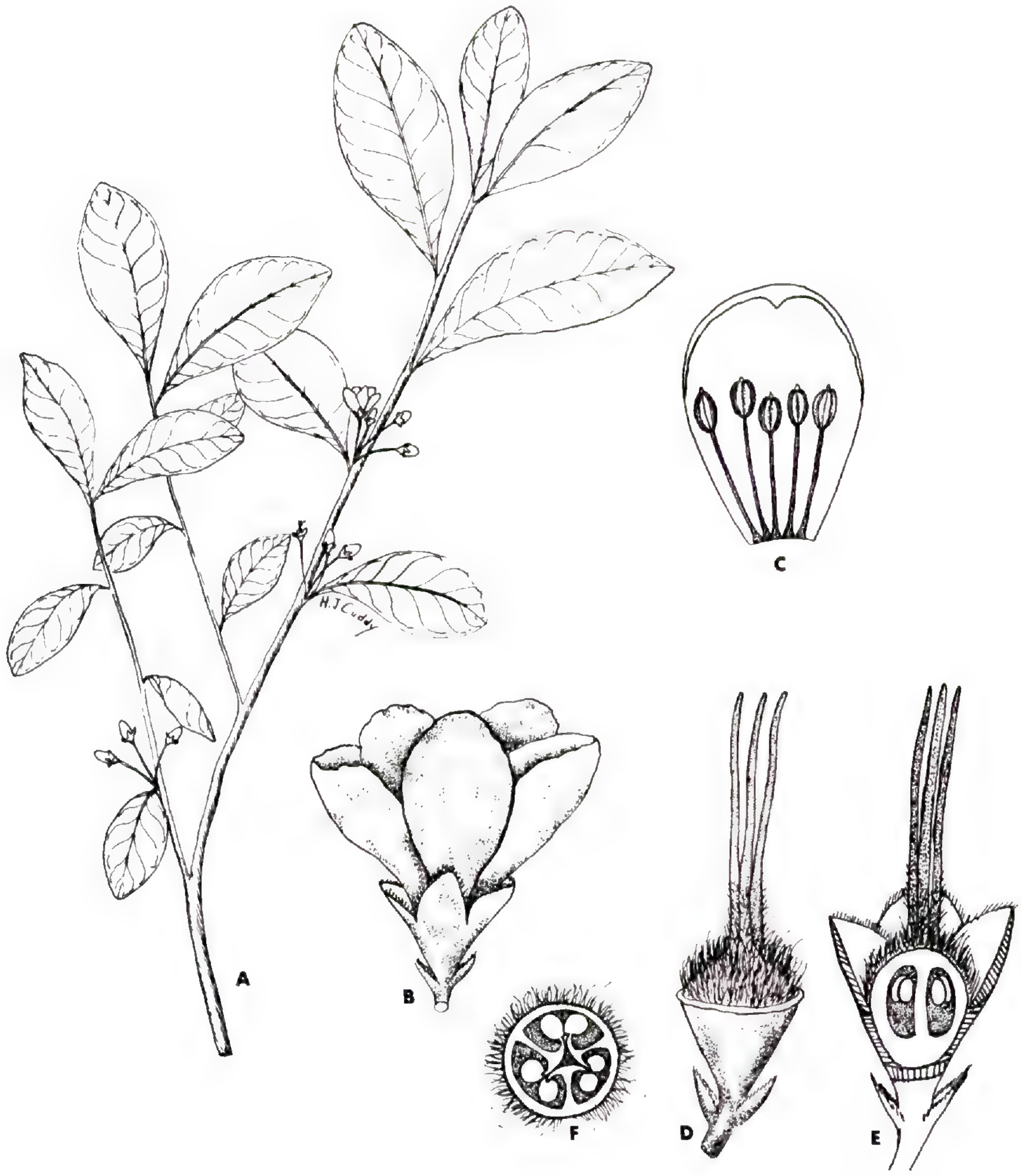

Fig. 4. *Symplococarpon chiriquense* Kobuski: A, habit (×½); B, flower (×3); C, petal and 5 stamens (×4); D, gynoecium (×8); E, id., longitudinal section (×8); F, id., cross-section (×8). After *Davidson 799* (F).

the apex; petals cream-colored, broadly elliptic-obovate, rounded, to 7-8 mm long and 6 mm wide; stamens 22-25, the filaments slightly enlarged at the base, to 3-3.5 mm long; ovary almost completely inferior, the upper part densely whitish-hirsute, 2- or 3-celled, with 2 ovules in each cell; styles 2 or 3, free almost to the base, ca 3 mm long, the base whitish-hirsute. *Fruits* unknown.

Known only from the type collection.

CHIRIQUÍ: Boquete, alt 5000 ft, *Davidson 799* (holotype F).

5. CLEYERA

Cleyera Thunberg, Nov. Gen. Pl. 68, 1783.

Trees or shrubs. *Leaves* alternate, the margins entire to serrulate, persistent or deciduous. *Flowers* solitary or fasciculate in the leaf axils, ☿, pedicellate, 2-bracteolate, the bracteoles subopposite or alternate, inserted near the apex of the pedicel, soon caducous; sepals 5, unequal, connate at the very base, usually ciliolate along the margins, persistent; petals 5, alternisepalous, connate slightly at the very base; stamens ca 25, 1-seriate, adnate to the base of the corolla, the anthers basifixed, setose; ovary superior, 2-3-celled, each cell ∞-ovulate, the styles united into one, the stigmas 2-3. *Fruits* baccate, globose to ovoid, ∞-seeded; seeds with thin endosperm, the embryo curved.

A small neotropical genus of about 10 species distributed in Mexico, Central America, and mainly in the West Indies; *C. japonica* Thunberg emend. Siebold & Zucc., the type species of the genus, is the only species occurring in Asia (Japan, Korea, China); one species reported from Panama and Central America.

Useful reference:

Kobuski, C. E. Studies in the *Theaceae*, VII. The American species of the genus *Cleyera*. Jour. Arnold Arb. **22:** 395-416, 1941.

1. **Cleyera theaeoides** (Sw.) Choisy, Mém. Soc. Phys. Hist. Nat. Genève **14**(1): 110, 1855; Williams, Fieldiana: Bot. **29:** 353, 1961.—Fig. 5.

Eroteum theaeoides Sw., Nov. Gen. Sp. Pl. Prodr. **85,** 1788.
Eurya panamensis Standley, Ann. Missouri Bot. Gard. **25:** 829, 1938.
Cleyera panamensis (Standley) Kobuski, Jour. Arnold Arb. **22:** 412, 1941.

Trees or sometimes shrubs, 5-18 m high, the branchlets minutely puberulous to glabrous. *Leaves* with the petiole to 1 cm long, canaliculate above, puberulous to glabrous beneath; blade obovate or elliptic-obovate, attenuate and decurrent at the base, rounded to obtuse to obtusely caudate at the apex, often also submarginate, to 10 cm long and 4.5 cm wide, rigid-membranous to subcoriaceous, the margins subrevolute, entire along the lower ¼, distinctly to obscurely serrulate along the upper ¾, glabrous above, sparsely puberulous to glabrescent beneath, the midvein prominent beneath, the lateral veins prominulous beneath. *Flowers* solitary or in fascicles of 3-4, the pedicels slender, to 22 mm long, the bracteoles inserted immediately below the calyx, subopposite, to 2 mm long; sepals subcircular, to 4 mm long, minutely ciliolate along the margins, glabrous or sometimes sparsely puberulous dorsally; petals white or yellow, obovate, rounded and ± reflexed at the apex, ca 6 cm long; stamens adnate to the base of the petals, to 3 mm long; ovary ellipsoid, ca 2.5 mm long, glabrous, the style ca 2.5 mm long. *Bacca* subglobose, 8-12 mm in diam, surmounted by the wholly or partially persistent style.

Mexico, Central America, and Jamaica; at high altitudes.

CHIRIQUÍ: valley of upper Río Chiriquí Viejo, alt 1300-1900 m, *White & White 16* (type *C. panamensis*, F, MO, NY, US); Volcán de Chiriquí, alt 7000-9000 ft, *Davidson 880* (F, MO, US), *1350* (F, MO); vic of Callejón Seco, Volcán de Chiriquí, alt 1700 m, *Wood-*

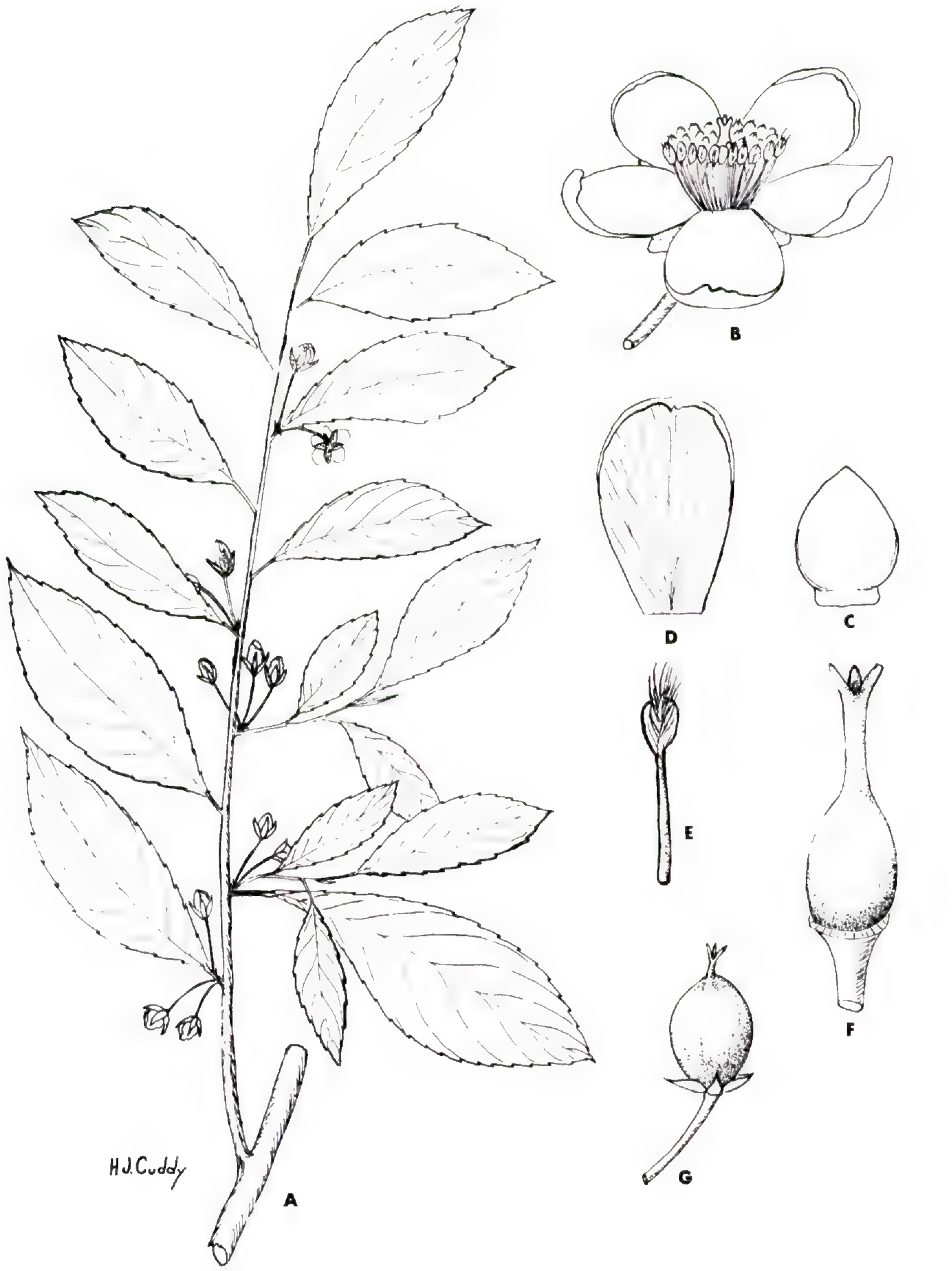

Fig. 5. *Cleyera theaeoides* (Sw.) Choisy: A, habit (×½); B, flower (×3); C, sepal (×4); D, petal (×4); E, stamen (×6); F, gynoecium (×6); G, bacca (×1). A-F after *Blum & Dwyer 2550* (MO); G after *Davidson 1350* (MO).

son & Schery 499 (MO); vic of Casita alta, Volcán de Chiriquí, alt ca 1500-2000 m, *Woodson et al. 791* (F, MO, NY, US); vic of Finca Lérida, alt 1750 m, *Woodson & Schery 232* (MO); id., upper forested southern slopes of the Quebrada Velo, alt 5000 ft, *Allen 4734* (MO, US); Boquete, alt 5000-5500 ft, open hillsides, *Davidson 771* (F, MO, US), 785 (F); Finca Collins, vic of Boquete, *Blum & Dwyer 2550* (MO); Bajo Chorro, rain forest, alt 6000 ft, *Davidson 384* (F, MO, US).

6. TERNSTROEMIA

Ternstroemia Mutis ex L. f., Suppl. Pl. Syst. Veg. 39, 264, 1781, nom. gen. conserv.

Mokof Adanson, Fam. Pl. **2:** 501, 1763.
Taonabo Aubl., Hist. Pl. Gui. Fr. 569, 1775.

Trees or shrubs, the branches ± opposite or verticillate, glabrous. *Leaves* alternate, opposite or subverticillate, usually coriaceous, the margins entire or nearly so. *Flowers* axillary, usually solitary, ☿, the bracteoles usually 2, opposite or subopposite, mostly inserted immediately beneath the calyx, sepaloid; sepals 5, imbricate, persistent; petals 5, imbricate, episepalous, distinct or ± connate basally, deciduous; stamens ∞, usually 2-seriate, the filaments united at the base and adnate to the corolla, the anthers basifixed, glabrous, usually longer than the filaments, the connective usually projected into an apiculate or caudate appendage; ovary superior, usually 2-3-celled, the ovules 2-20 in each cell, pendulous; styles united into one, the stigma entire. *Fruits* baccate, soft-coriaceous, often crowned by the persistent style, few-seeded, the testa smooth or papillate; endosperm scanty, fleshy; embryo curved.

A genus of about 85 species, mostly in tropical America and Asia; one species in tropical Africa (Angola); only one species reported from Panama.

Useful references:

Kobuski, C. E. Studies in the *Theaceae,* XII. Notes on the South American species of *Ternstroemia.* Jour. Arnold Arb. **23:** 298-343, 1942.

————. Studies in the *Theaceae,* XIII. Notes on the Mexican and Central American species of *Ternstroemia.* Jour. Arnold Arb. **23:** 464-478, 1942.

1. **Ternstroemia tepezapote** Schlecht. & Cham., Linnaea **6:** 420, 1831.—Fig. 6.

T. peduncularis Seemann, Bot. Voy. Herald 87, 1853, non DC. (Mém. Soc. Phys. Hist. Nat. Genève **1:** 409, 1822).
T. seemannii Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **18:** 260, 1862.
Nokofua seemannii (Triana & Planchon) O. Ktze., Rev. Gen. Pl. **1:** 63, 1891.
Taonabo seemannii (Triana & Planchon) Standley, Jour. Wash. Acad. Sci. **15:** 459, 1925.

Trees, sometimes shrubs, 2-20 m tall, the trunk to 60 cm in diam, the bark reddish-brown. *Leaves* grouped towards the apex of the branchlets, the petiole to 1.5 cm long, canaliculate above; blade obovate, oblong-obovate, or narrowly obovate, long-attenuate at the base, obtusely acuminate to sometimes obtuse at the apex, to 12 cm long and 5 cm wide, rigid-chartaceous to coriaceous, the margins plane to subrevolute and mostly entire, the midvein ± impressed above and prominent below, the lateral veins inconspicuous on both surfaces. *Flowers* axillary, solitary, the pedicels terete, 2-5 cm long, the bracteoles inserted just below the calyx, op-

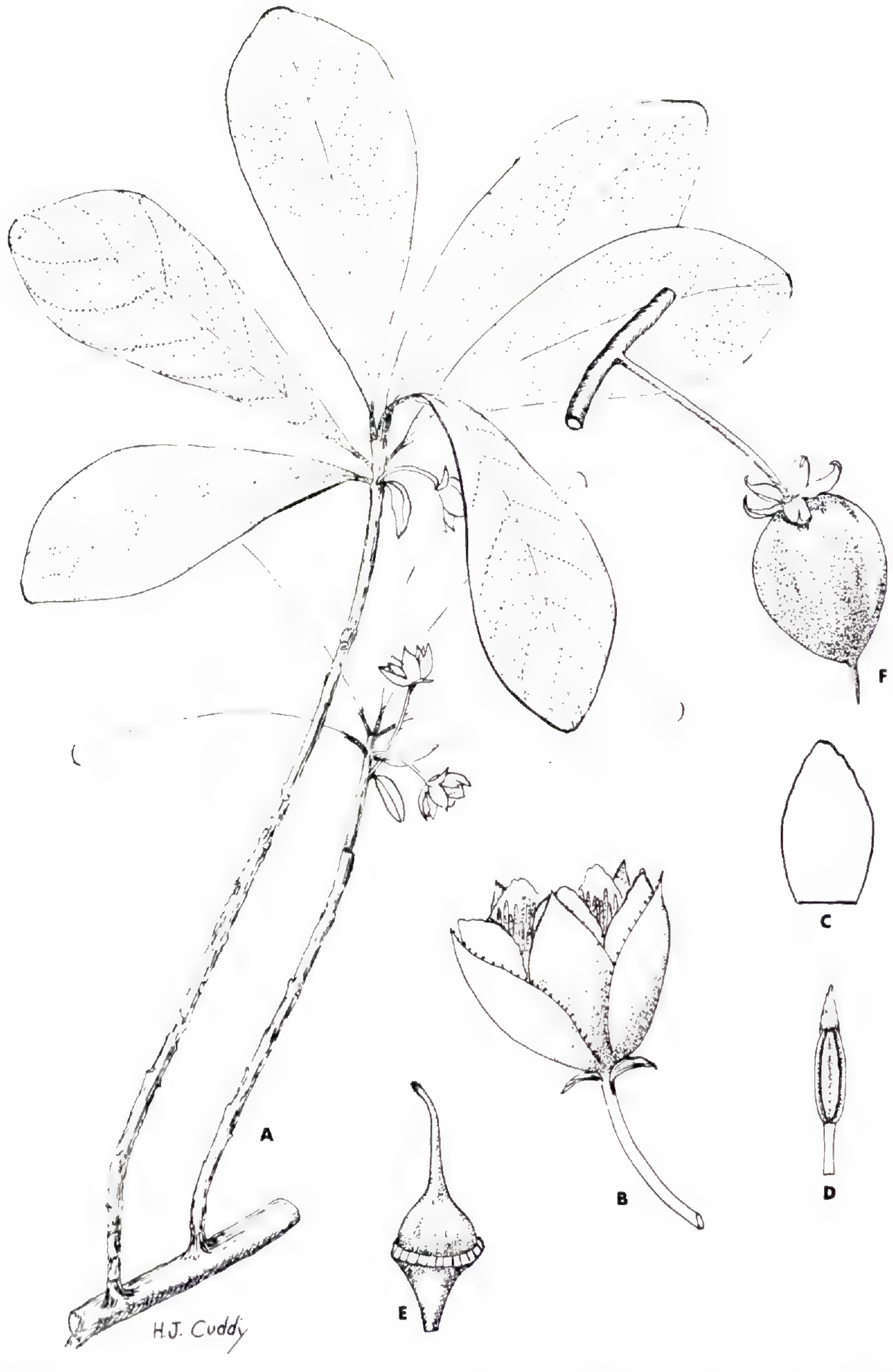

Fig. 6. *Ternstroemia tepezapote* Schlecht. & Cham.: A, habit (×½); B, flower (×2); C, petal (×2); D, stamen (×4); E, gynoecium (×2); F, bacca (×1). A-E after *Tyson 3641* (MO); F after *Johnston 1610* (MO).

posite, unequal, ovate to subcircular, to 4 mm long, the margins entire to glandular-denticulate; sepals unequal, subcircular to broadly ovate, rounded or acute to apiculate at the apex, to 10 mm long, white or greenish-white, the margin scarious, the outer ones entire-margined or sometimes conspicuously glandular-denticulate; petals white, yellow at the apex, ovate, as long as or slightly shorter than the calyx, connate at the base of the petals, to 1.5 mm long, the anthers narrowly oblong, to 2 mm long, the connective projected into an appendage 1-1.75 mm long; ovary conical, 2-celled, each cell 4-5-ovulate, the style to 7 mm long, the stigma punctiform. *Bacca* broadly ovoid, commonly surmounted by a slender stylar beak, to 1.8 cm long and wide, brownish, bursting irregularly at maturity; seeds few, scarlet, to 10 mm long.

Mexico and Central America.

The flowers have a pleasant anise-like odor (cf. *Duke 8059*). Colloquial names reported from Panama are *manglillo de boton* (cf. *Stern et al. 1749*) and *manzanilla de sabana* (*Bro. Maurice 787*).

Kobuski (loc. cit. 467-468) recognizes as a distinct species *T. seemannii* because the outer calyx lobes are entire-margined, while they are glandular-denticulate in *T. tepezapote*. This character, however, seems to be a very variable one. Standley & Williams, in the Flora of Guatemala (Fieldiana: Bot. **24**(7): 34, 1961), describe the calyx lobes of *T. tepezapote* as "glandular-denticulate, often conspicuously so, or sometimes entire." As the same variation seems to occur throughout the range of *T. tepezapote*, I have reduced *T. seemannii* to synonymy.

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 1135* (MO, US). CANAL ZONE: Chagres, Isthmus of Panama, *Fendler 317* (syntype *T. seemanii*, MO, US); along rd 2 mi SW of Fort Sherman, *Johnston 1610* (MO); Barro Colorado I, *Shattuck 783* (F, MO), *860* (F, MO), *1092* (F, MO, US), *1159* (F, MO), *Wilson 132* (F), *Woodworth & Vestal 686* (F); hill nr summit of Trans-Isthmian Hwy, *Harvey 5288* (F). CHIRIQUÍ: trail from San Felix to Cerro Flor, alt 100-850, *Allen 1931* (MO). COCLÉ: Penonomé & vic, alt 50-1000 ft, *Williams 374* (NY, US); hills S of El Valle de Antón, alt ca 700 m, *Allen 2473* (MO, NY, US); betw Las Margaritas & El Valle, *Woodson et al. 1300* (F, MO, NY). COLÓN: Loma de la Gloria, nr Fató (Nombre de Dios), in forests, alt 10-104 m, *Pittier 4079* (NY, US). DARIEN: forest nr Pidiaque peak, alt 800-1000 ft, *Duke 8059* (MO). HERRERA: rd betw Ocú & Las Minas, along rd cut, *Stern et al. 1749* (MO, US). PANAMA: Cerro Campana, *Ebinger 374* (MO); Arraijan, alt 50 m, in dense shade, *Allen 732* (F, MO, NY, US); thickets & forests nr Arraijan, alt ca 15 m, *Woodson et al. 1340* (F, MO, NY); Sabanas N of Panama City, *Bro. Paul 416* (US); Juan Díaz, moist woods, common, *Standley 30585* (US); 1 mi N of Cerro Azul, alt 2300 ft, *Tyson & Blum 4070* (MO); Cerro Azul, alt 2000 ft, nr lake, *Tyson & Blum 4057* (MO); Pacora, llanos above village, alt below 300 ft, *Bro. Maurice 787* (US); San José I, *Erlanson 43* (US), *93* (US), *Johnston 409* (MO, US), *622* (MO, US). VERAGUAS: Canazas, common on dry hills, *Tyson 3641* (MO); Isla de Coiba (Colonia Penal), along beach, *Dwyer 2372* (MO). PROVINCE UNKNOWN: *Hayes 931* (NY).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 125. BIXACEAE[1]

BY ANDRÉ ROBYNS[2, 3]

Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Shrubs or small trees, with reddish-orange sap. *Leaves* alternate, long-petiolate, stipulate, the blade simple, palminerved. *Inflorescences* terminal, paniculate. *Flowers* ☿, actinomorphic; pedicel bearing 5 conspicuous glands below the calyx; sepals 5, distinct, imbricate, fugacious; petals 5, distinct, imbricate, white or pink, fugacious; stamens ∞, distinct, inserted on a thick receptacle, the anthers 2-thecate, hippocrepiform, apically dehiscent by 2 narrow slits; pollen 3-colporate, the sexine reticulate or striate-reticulate; gynoecium with 2 syncarpous carpels, the ovary superior, 1-locular, with 2 parietal placentae, the ovules ∞, anatropous, the style simple, the stigma shortly 2-lobulate. *Fruits* capsular, loculicidally 2-valvate, the pericarp densely covered with flexible spines to nearly unarmed; seeds numerous, with fleshy, reddish testa, the endosperm copious, the embryo straight.

A monogeneric family native to tropical America.

BIXA

Bixa L., Sp. Pl. 512, 1753; Gen. Pl. ed. 5, 228, 1754.

Characters of the family.

A small genus with only one species in Panama and Central America.

1. **Bixa orellana** L., Sp. Pl. 512, 1753.—Fig. 1.

Shrub or tree, usually evergreen, 1.5-10 (15) m tall, the trunk up to 10 cm in diam, the bark lenticellate, the branchlets covered with minute, reddish-brown scales. *Leaves* with the petioles slender, terete, slightly enlarged at the apex, 1.8-14 cm long, ± densely covered with minute scales, the stipules narrowly ovate, acuminate at the apex, ca 1 cm long, fugacious; blade ovate or sometimes ovate-

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[1] Assisted by National Science Foundation Grant No. GB-170 (Principal Investigator, H. C. Cutler).

[2] Visiting Curator of the Flora of Panama, Missouri Botanical Garden; *Chargé de Recherche* of the National Foundation for Scientific Research, Belgium.

[3] I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and for the loan of material: Field Museum of Natural History, Chicago, Illinois (F) and U. S. National Herbarium, Washington, D. C. (US).

triangular, infrequently oblong-ovate, the base truncate or truncate-subcordate or rounded or rounded-subcordate, the apex sometimes acute to generally gradually long-acuminate and with the acumen usually blunt and often inconspicuously mucronulate, entire-margined, 5.5-27 cm long and 3-18 cm wide, membranous to chartaceous, 5-palminerved, slightly discolor, the upper surface usually ± shining and glabrous or sparsely lepidote especially when young and along the veins, the lower surface dull, paler, ± densely lepidote, and with the main veins and secondary veins prominent. *Panicles* small to large, few- to many-flowered, the axes densely covered with minute, reddish-brown scales, the bracts and bracteoles squamiform and fugacious. *Flowers* with the pedicels up to 1 cm long, densely covered with minute, reddish-brown scales; sepals circular, cucullate, 7-9 mm in diam, densely lepidote outside; petals obovate, rounded at the apex, 20-33 mm long and 8-20 mm wide, white or pink; androecium ca 14-15 mm long, the filaments filiform, the anthers ca 1-1.5 mm long; ovary more or less globose to pyriform, densely to sparsely bristly, the style up to 15 mm long, slightly enlarged towards the apex, glabrous. *Capsules* very variable in shape, size, and indumentum, oblong-ovoid to ovoid to globose to ± reniform to transversely ellipsoid, ± flattended or not, rounded to acute or sometimes acuminate at the apex, 1.3-4.5 cm long and 1.3-4 cm broad, brown to flaming red, densely to sparsely covered with long or sometimes short, flexible spines, sometimes nearly smooth; seeds obovoid-angular, ca 5 mm long, the testa densely reddish-orange papillate.

Native to and widely distributed throughout continental tropical America; planted and naturalized in tropical and subtropical regions of the world; known locally as *achote* or *achiote*.

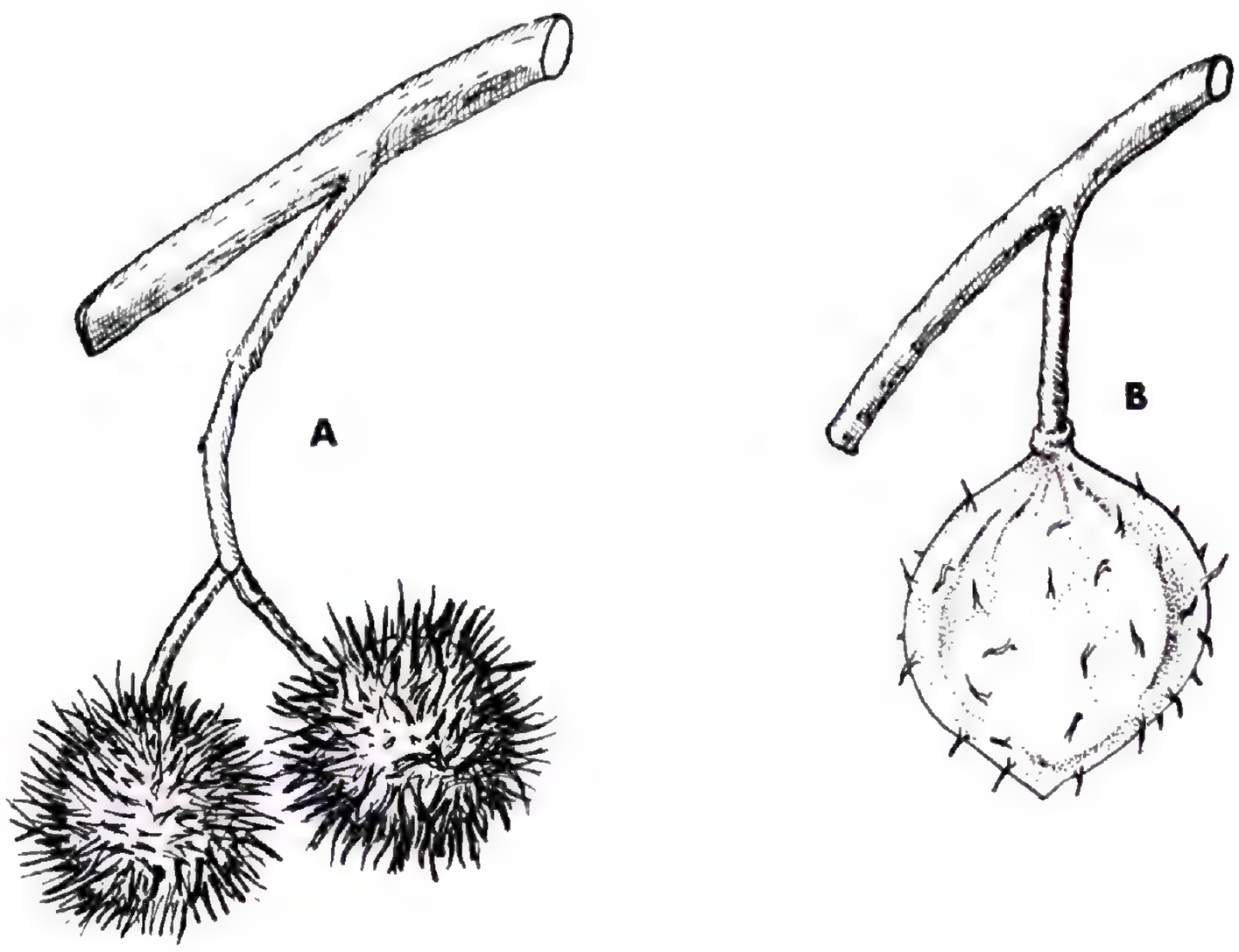

Fig. 1. *Bixa orellana* L.: Capsules (×⅔). A after *Dwyer & Robyns* 68 (MO); B after *Dwyer 3109* (MO).

BOCAS DEL TORO: Changuinola Valley, in abandoned land, *Dunlap 242* (F, US); Changuinola to 5 mi S at junction of Ríos Changuinola & Terebé, *Lewis et al. 945* (MO); Isla Colón, *von Wedel 1299* (MO); Old Bank I, *von Wedel 2092* (MO, US); Water Valley, *von Wedel 1642* (MO, US); vic of Chiriquí Lagoon, *von Wedel 1326* (MO). CANAL ZONE: Chagres, *Fendler 328* (MO, US); Barro Colorado I, *Shattuck 340* (F), *703* (F), *Wetmore & Abbe 130* (F), *Wilson 150* (F), *Woodworth & Vestal 525* (F); along Chagres River, NW of Gamboa, *Dwyer & Robyns 68* (MO); along Río Chagres betw Gamboa & Alhajuela, alt 30-60 m, *Allen 957* (F, MO, US); in Government forest along Las Cruces Trail, alt 75 m, *Hunter & Allen 718* (MO); Culebra Cut, *Gaillard s.n.* (US); Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5764* (US); vic of Miraflores, *White 127* (F, MO); vic of Río Cocoli, Rd K-9, nr bridge along rd, few ft from stream, *Stern et al. 311* (MO, US); nr Rodman Base, *Dwyer 2669* (MO); Rd C-21, *Duke 5778* (MO); s. loc., *Johansen 69* (US). CHIRIQUÍ: Río San Cristobal, 2 mi W of David, alt 150 ft, *Tyson 915* (MO). COLÓN: betw France Field, Canal Zone, & Catival, moist thicket, *Standley 30317* (US); Juan Minas plantation, Río Chagres, region above Gamboa, alt 25 m, *Allen 4111* (MO); Achiote, *Tyson et al. 4504* (MO). DARIEN: ca 10 mi S of El Real on Río Pirre, *Duke 5476* (MO); vic of Pinogana, *Allen 936* (F, MO, US). HERRERA: 10 mi S of Ocú, *Tyson et al. 2821* (MO). LOS SANTOS: Pocri, *Dwyer 1214* (MO); Punta Mala, *Tyson 2731* (MO). PANAMA: rd to San Carlos, *Harvey 5140* (F); along Río Chilibre, *Piper 5665* (US); betw Matías Hernández & Juan Díaz, *Standley 31969* (US); Tocumen, *Dwyer 3100* (MO), *4430A* (MO); Río Tocumen, moist forest, *Standley 26751* (US); banks of Mamoni River, below La Capitano, alt 20-25 m, *Pittier 4581* (F, US); Río Bayano, nr crossing of Pan-Amer Hwy, above confluence with Río Chepo, *Duke 3982* (MO); along rd betw Panama City & Chepo, *Dodge et al. 16630* (MO); Taboga I, moist thicket, *Standley 27879* (US). VERAGUAS: ca 5 mi N of Santiago, vic of Santa Maria River, *Blum & Tyson 595* (MO); Santiago, *Dwyer 1357* (MO).

Bixa orellana is highly variable especially regarding the form, size, and indumentum of the capsules. Among the Panamanian material the following varieties can be recognized: the var. *urucurana* (Willd.) O. Ktze. ex Pilger (in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, **21:** 315, 1925) characterized by the rather small, globose to ± reniform or transversely ellipsoid capsules densely covered with long, flexible spines, and the var. *leiocarpa* (O. Ktze.) Standley & Williams (Fieldiana: Bot. **29:** 358, 1961) with ± flattened, ellipsoid, nearly unarmed capsules. An exhaustive study of all available herbarium material is greatly needed in order to evaluate these fruit variations.

The plant is important for the reddish-orange dye obtained from the fleshy testa of the seeds and commercially known as annatto. This is used for coloring food, especially rice, margarine, butter, cheese, soups, etc., and for coloring oils, varnishes and cosmetics. The Indians paint their faces and bodies with it, "partly for adornment and partly for relief from gnats, mosquitoes, and other insects" (cf. Standley, Contr. U. S. Nat. Herb. **27:** 270, 1928).

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Numbers in **boldface** type refer to descriptions; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 126. COCHLOSPERMACEAE[1]

BY ANDRÉ ROBYNS[2, 3]

Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Herbs, rhizomatous, or shrubs, or small trees, with colored sap. *Leaves* alternate, stipulate, the blade palmatilobed or compound-digitate, the margins entire to serrate. *Inflorescences* racemose or paniculate, the flowers usually appearing before the leaves. *Flowers* ☿, actinomorphic, usually large and showy; sepals 4-5, imbricate, distinct, caducous or long-persistent; petals 4-5, imbricate or convolute, distinct, caducous; stamens ∞, the filaments distinct, equal in length or unequal, the anthers basi- or dorsifixed, linear, 2-thecate, apically poricidal or dehiscing by apical, short slits; pollen grains usually 3-colporate; gynoecium with 3-5 syncarpous carpels; ovary superior, 1-locular, or the placentae intruding and falsely or at the base only 3-5-locular, the placentation accordingly parietal or axile, the ovules ∞, anatropous; style 1, the stigma small, denticulate or lobulate. *Fruits* capsular, loculicidal, 3-5-valvate, the endocarp thick and separating from the thin endocarp; seeds ∞, straight or reniform, glabrous or long-lanate; albumen copious and oily; embryo curved; cotyledons large and foliaceous.

A small, tropical family of three genera, with only the following genus reported from Panama.

1. COCHLOSPERMUM

Cochlospermum Kunth, *Malvac.* 6, 1822, nom. nud.; Kunth in H.B.K., Nov. Gen. Sp. Pl. **5:** 297, 1822, nom. gen. conserv. (see also A. Robyns, Ann. Missouri Bot. Gard. **53:** 113, 1966).

Maximilianea Mart. in Schrank, Flora **2:** 452, 1819.

Suffrutices, shrubs or small trees, deciduous, sometimes with tuberous roots. *Leaves* petiolate, palmatilobed or compound-digitate, glabrous or not. *Inflorescences*

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[1] Assisted by National Science Foundation Grant No. GB-170 (Principal Investigator, H. C. Cutler).

[2] Visiting Curator of the Flora of Panama, Missouri Botanical Garden; *Chargé de Recherche* of the National Foundation for Scientific Research, Belgium.

[3] I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and for the loan of material: Field Museum of Natural History, Chicago, Illinois (F) and U. S. National Herbarium, Washington, D. C. (US).

terminal and axillary, racemose or paniculate. *Flowers* 5-merous, the sepals unequal; petals convolute, large, membranous, mostly yellow; filaments slender, equal or not, the anthers basifixed, oblong or linear, apically poricidal; ovary 1-locular except at the base, with 3-5 parietal placentae; style slender, the stigma scarcely thickened, usually inconspicously denticulate. *Capsules* 1-locular, the exocarp glabrous or not, the endocarp membranous; seeds reniform, long-lanate, the testa thin and easily detachable.

A pantropical genus of about 15 species, the majority in South America; only one species in Panama as well as in North America.

1. **Cochlospermum vitifolium** (Willd.) Spreng. in L., Syst. Veg. ed. 16, **2:** 596, 1825.—Fig. 1.

Bombax vitifolium Willd., Enum. Pl. Hort. Reg. Bot. Berol. 720, 1809.
Cochlospermum hibiscoides Kunth, Syn. Pl. Aequin. **3:** 214, 1824.
Wittelsbachia vitifolia (Willd.) Mart. in Mart. & Zucc., Nov. Gen. Sp. Pl. **1:** 82, 1824.
Maximilianea hibiscoides (Kunth) O. Ktze., Rev. Gen. Pl. **1:** 44, 1891.
M. vitifolia (Willd.) Krug & Urb., Engl. Bot. Jahrb. **15:** 293, 1892; Blake, Jour. Wash. Acad. Sci. **11:** 128, 1921.

Tree 5-12 m high, the trunk 5-10 cm in diam, relatively few-branched, the branchlets minutely puberulous, becoming glabrous. *Leaves* with the petioles slender, to 30 cm long, minutely puberulous when young, the stipules small, subulate, soon caducous; blade cordate-subcircular in outline, usually (3-)5-palmatifid, sometimes (3-)5-palmatilobed, to 30 cm in diam, the lobes with acute to obtuse sinuses, with the apex acute to long-caudate or long-acuminate and minutely mucronulate, with the margins from distinctly crenate to crenulate-serrulate to subentire, and with the midvein prominent beneath, the upper surface slightly shiny and glabrous, the lower surface somewhat paler and finely puberulous especially along the veins to nearly glabrous. *Inflorescences* terminal and paniculate, the panicles erect and spreading. *Flowers* with the pedicels to 3 cm long, slightly elongated in fruit, puberulous; calyx subcoriaceous, minutely tomentellous and sparsely puberulous, the 2 outer sepals ovate to oblong-obovate, rounded (to sometimes acute?) at the apex, 12-18 mm long and 7-9 mm wide, the 3 inner sepals largely obovate to subrotund, rounded at the apex, 20-22 mm long and 16-20 mm wide; petals obovate, 5-6 cm long, yellow; filaments unequal, 8-20 mm long, glabrous, the anthers oblong-linear, ca 4-6 mm long; ovary subglobose, ca 7-8 mm in diam, puberulous; style to 35 mm long, glabrous. *Capsules* obovoid-ellipsoid, umbilicate, 5-valved, to 8 cm long, grayish-velvety-tomentellous; seeds reniform, 4-5 mm long, dark brown, densely whitish long-lanate.

Mexico, Central America and northern South America; very common about the Canal Zone in Panama, especially on brushy hillsides (cf. Standley, Contr. U. S. Nat. Herb. **27:** 270-271, 1928); known locally as *poro-poro;* often cultivated.

CANAL ZONE: Chagres, *Fendler 307* (F, MO); betw Chagres Batteries & Fort San Lorenzo, *Maxon & Valentine 6998* (US); nr Fort Randolph, swampy woods, *Standley 28609* (US); Gatun, moist situation, *Riley 107* (US); Barro Colorado I, *Kenoyer 652* (US), *Westmore & Abbe 277* (F), *Wilson 110* (F), *Woodworth & Vestal 649* (F); Frijoles, *Ebinger 318* (MO); Gamboa, open field, *Standley 28468* (US); Obispo, in thicket, *Standley*

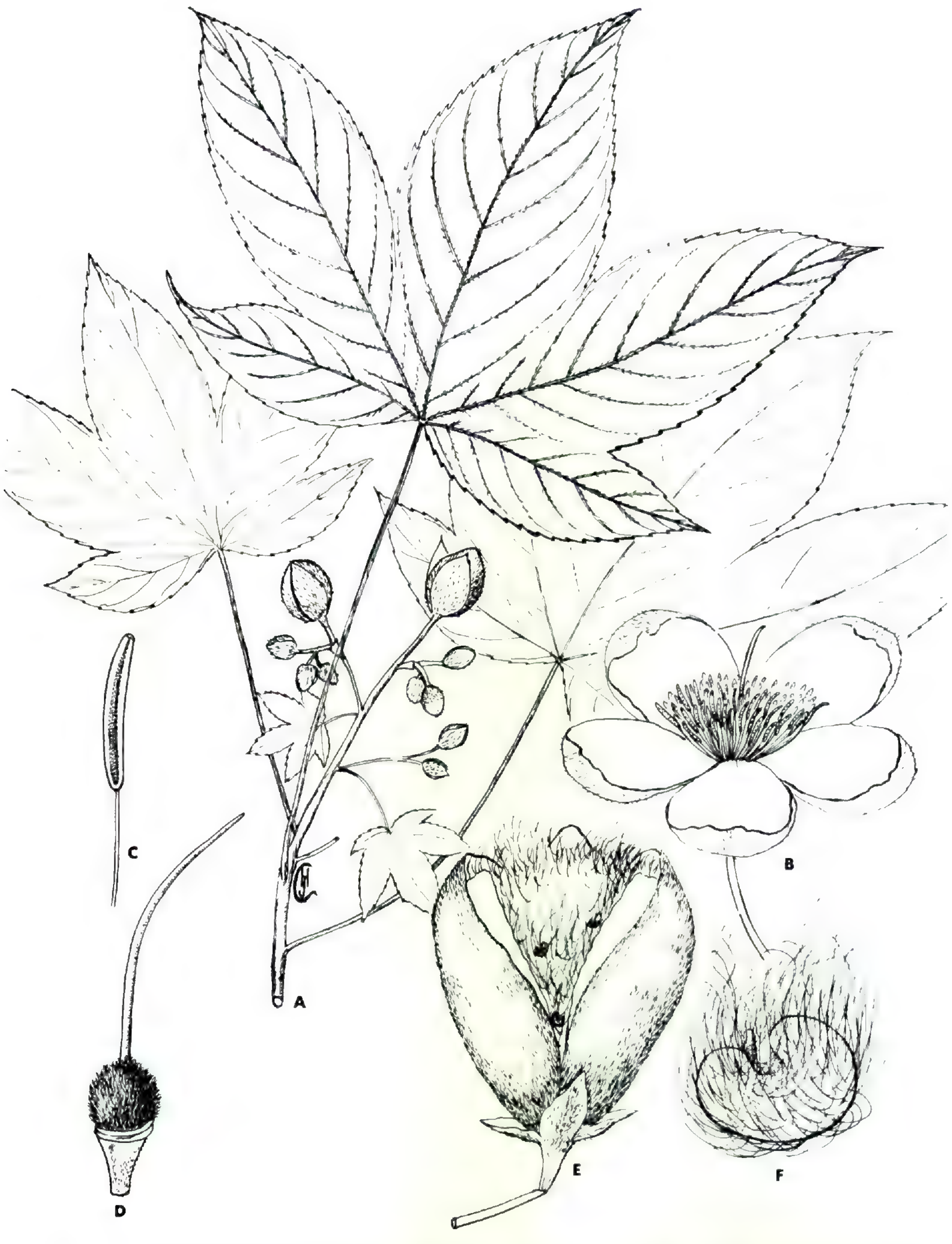

Fig. 1. *Cochlospermum vitifolium* (Willd.) Spreng.: A, habit (×½); B, flower (×½); C, anther (×4); D, gynoecium (×1); E, dehiscent capsule (×½); F, seed (×5). A-D after *Tyson 2630* (MO); E-F after *Godfrey 67015* (MO), Costa Rica.

31661 (US); betw Summit & Gamboa, *Greenman & Greenman* 5222 (MO); thickets N of Summit, *Woodson et al.* 767 (MO); Las Cascadas Plantation, nr Summit, wet thicket, *Standley* 25799 (US); vic of Summit, brushy slope, *Standley* 30052 (US); Cerro Gordo, nr Culebra, alt 50-290 m, *Pittier* 2316 (US); Chiva-Chiva Trail, 2 mi above Red Tank, roadside, *Maxon & Harvey* 6603 (US); W side of Canal opposite Miraflores, *Dorothy R. Harvey* 5225 (F); vic of Río Cocoli, Rd K-9, in cut-over area, *Stern et al.* 9 (MO); Fort Clayton, nr chemical test area, *Tyson* 2630 (MO); id., Cardenas Creek area, *Tyson* 3456 (MO); along old Las Cruces Trail, betw Fort Clayton & Corozal, moist thicket, *Standley* 29126 (US); in Government forest along Las Cruces Trail, alt 75 m, *Hunter & Allen* 669 (MO); nr Corozal, *Greenman & Greenman* 5189 (MO); Balboa, moist thicket, *Standley* 25525 (US), *32126* (US); Ancon Hill, *Greenman & Greenman* 5110 (MO); betw Farfan Beach & Palo Seco, alt 5 m, *Hunter & Allen* 441 (MO); drowned forest of Quebrada Bonita, alt 70-80 m, *Dodge & Allen* 17067 (MO); drowned forest in valley of Río Puente betw the Tunnel & Natural Bridge, alt 70 m, *Dodge & Allen* 17318 (MO); s. loc., *Epplesheimer s.n.* (F), *Johansen* 14 (US), 47 (US). HERRERA: vic of Ocú, alt 100 m, *Allen* 4071 (MO). LOS SANTOS: Pocri, *Dwyer* 1198 (MO). PANAMA: vic of Arraijan, *Allen* 1620 (MO); vic of Bella Vista, *Piper* 5362 (US); Las Sabanas, *Bro. Celestine* 118 (US); betw Savanas & Río Yguana, *Macbride* 2672 (F, US); vic of Juan Franco Race Track, nr Panama City, moist thicket, *Standley* 27771 (US); nr Matías Hernández, moist thicket, *Standley* 28921 (US); betw Matías Hernández & Juan Díaz, dry thicket, *Standley* 32075 (US); Río Tapía, moist thicket, *Standley* 28078 (US); nr big swamp E of Río Tocumen, wet forest, *Standley* 26723 (US); Taboga I, moist thicket, *Standley* 27071 (US); San José I, thickets bordering Bald Hill, *Erlanson* 299 (US). PROVINCE UNKNOWN: *Hayes s.n.* (MO, US).

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Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 127. VIOLACEAE[1]

BY ANDRÉ ROBYNS[2, 3]

Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Herbs, annual or perennial, or shrubs, sometimes scandent, infrequently small trees. *Leaves* alternate, opposite or apparently opposite, usually stipulate, the blade simple, entire-margined to dentate, rarely ± dissected. *Inflorescences* axillary or terminal, spicate, racemose or paniculate, sometimes cymose, or flowers solitary or few in the axils. *Flowers* ☿, rarely ♂ ♀ or polygamous, actinomorphic or zygomorphic; pedicels usually articulate, bracteolate, the bracteoles mostly persistent; calyx quincuncial, the sepals 5, usually distinct, equal or not, usually persistent; corolla usually imbricate, the petals 5, distinct, equal to very unequal, the anterior petal often larger than the others and calcarate, saccate or gibbous at the base, deciduous or not; stamens 5, alternipetalous, similar or not, the filaments free or ± connate, the 2 anterior filaments in zygomorphic flowers with dorsal appendages which project into the spur, the anthers free or connivent or connate, introrse, 2-thecate, usually longitudinally dehiscent, the connectives often dilated into membranous appendages; pollen usually 3-colporate; gynoecium (2) 3 (4-5)-carpellate, syncarpous; ovary superior, 1-locular, with (2) 3 (4-5) parietal placentae each bearing 1-∞ anatropous ovules; style simple, terminal, sometimes geniculate below, often clavate above, the style apex variously shaped, the stigma usually simple. *Fruit* a loculicidal capsule usually with 3 elastic, dorsally carinate valves, rarely baccate or nut-like; seeds often carunculate, usually with copious endosperm.

A family of 16-18 genera and 850 species distributed all over the world, but particularly well developed in tropical regions; six genera at present reported from Panama.

The family has no economic significance, except for the predominantly temperate genus *Viola* L. of which several species are of ornamental value.

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[1] Assisted by National Science Foundation Grant No. GB-170 (Principal Investigator, H. C. Cutler).

[2] Visiting Curator of the Flora of Panama, Missouri Botanical Garden; *Chargé de Recherche* of the National Foundation for Scientific Research, Belgium.

[3] I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and for the loan of material: Field Museum of Natural History, Chicago, Illinois (F) and U. S. National Herbarium, Washington, D. C. (US).

Useful reference:

Melchior, H., *Violaceae* in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, **21:** 329-377, 1925.

a. Flowers actinomorphic or slightly zygomorphic; anterior petal not saccate or calcarate; stamens similar or almost so.
  b. Flowers actinomorphic; petals equal or almost so.
    c. Fruit capsular ..... 1. *Rinorea*
    cc. Fruit baccate ..... 2. *Gloeospermum*
  bb. Flowers slightly zygomorphic; anterior petal ca twice as broad as the others ..... 3. *Amphirrhox*

aa. Flowers markedly zygomorphic; anterior petal saccate or calcarate; 2 anterior stamens with the filaments bearing dorsal, nectariferous appendages.
  d. Anterior petal unguiculate, the claw gibbous-saccate or shortly calcarate ..... 4. *Hybanthus*
  dd. Anterior petal calcarate.
    e. Sepals without basal auricles ..... 5. *Corynostylis*
    ee. Sepals basally auricled ..... 6. *Viola*

1. RINOREA

Rinorea Aubl., Hist. Pl. Gui. Fr. 235, 1775.

Alsodeia Du Petit-Thouars, Hist. Vég. Isl. Austr. Afr. 55, 1806.

Shrubs or small trees. *Leaves* alternate or apparently opposite, infrequently ternate, the stipules small and deciduous, the blade entire-margined to serrate. *Inflorescences* axillary or terminal, racemose, paniculate, or sometimes cymose, infrequently flowers solitary. *Flowers* small, actinomorphic, the pedicels articulate, bracteolate; sepals free, equal or slightly unequal, ciliolate along the margins, usually persistent; petals imbricate, free, equal or almost so, sessile or very shortly unguiculate, mostly reflexed at the apex, white, yellow, or sometimes red; filaments usually bearing dorsal, erect, carnose, glandular appendages, these adnate only basally or throughout their length to the filaments and often ± united into a tube; anthers free, the connectives dilated dorsally from the base or from the apex into thin, scarious scales (connective scales) exceeding the anthers, the thecae sometimes also appendaged; ovary with 3 placentae, each bearing 1-3 or more ovules; style usually erect, the stigma terminal. *Capsules* loculicidally and elastically 3-valvate, the seeds few, glabrous or pubescent, the endosperm copious and carnose.

A pantropical genus of about 250-300 species especially well represented in tropical Africa and characteristic of the rain forest; five species known from Panama.

Useful reference:

Blake, S. F., Revision of the American species of *Rinorea.* Contr. U. S. Nat. Herb. **20:** 491-518, *pl. 31-37*, 1924.

a. Leaves opposite; inflorescences racemose; connective dilated dorsally from the base into brownish scales.
  b. Leaf blades oblique and rounded to slightly cordate at the base; bracteoles exceeding the pedicels; sepals 3-4.5 mm long; petals slightly longer than the sepals; filaments without dorsal glands ..... 1. *R. sylvatica*

bb. Leaf blades acute to obtuse at the base; bracteoles shorter than the pedicels; sepals 1.1-2.5 mm long; petals twice as long as the sepals or longer; filaments with a dorsal gland.

c. Sepals 1.1-1.6 mm long; filaments ca 1 mm long; anthers with the thecae unappendaged; leaf blades narrowly obovate-elliptic to obovate-elliptic, or narrowly elliptic, chartaceous .....2. *R. squamata*

cc. Sepals 2-2.5 mm long; filaments scarcely 0.4 mm long; anthers with the thecae mucronate; leaf blades narrowly ovate, rigid-chartaceous .....3. *R. brachythrix*

aa. Leaves alternate; inflorescences contracted-racemose (or of contracted cincinni) or paniculate; connective dilated only at the apex into brownish or whitish scales.

d. Inflorescences paniculate; petals ca 3 mm long; dorsal glands of the filaments shorter than the filaments; connective scales broadly ovate, erose, brownish, exceeding the anthers by 0.5-0.8 mm; leaf blades narrowly elliptic to narrowly obovate or obovate, remotely repand-serrulate along the margins, rigid-chartaceous; tree .....4. *R. roureoides*

dd. Inflorescences contracted-racemose (or of contracted cincinni); petals up to 5 mm long; dorsal glands of the filaments about as long as the filaments; connective scales narrowly obovate-oblong, incised at the apex, whitish, exceeding the anthers by ca 1.5 mm; leaf blades narrowly ovate, entire-margined or almost so, membranous-chartaceous; shrub .....5. *R. blakeana*

1. **Rinorea sylvatica** (Seem.) O. Ktze., Rev. Gen. Pl. **1:** 42, 1891.

Alsodeia sylvatica Seem., Bot. Voy. Herald 79, *t. 14*, 1852.

Shrub or small tree, 1.5-3.6 m high, the branchlets puberulous and hirsute. *Leaves* opposite, the petiole up to 8 mm long, puberulous and hirsute, the stipules triangular, acuminate, up to 6 mm long; blade obovate to elliptic, oblique and rounded to slightly cordate at the base, acuminate at the apex, crenate or crenulate-serrulate to subentire at the margins, up to 16 cm long and 6.5 cm wide, chartaceous, hirsute especially along the prominent midvein below. *Racemes* terminal, up to 4 cm long, many-flowered, the rhachis densely rufous-hirsute, the hairs ± appressed. *Flowers* with the pedicels 2 mm long or less, rufous-hirtellous, the bracteoles exceeding the pedicels, broadly ovate to depressed ovate, acuminate-cuspidate, 2-3 mm long and 2-2.7 mm wide, dry, indurated, minutely ciliolate, appressed-hirtellous; sepals slightly unequal, ovate to broadly ovate, acuminate, cucullate, 3-4.5 mm long and 1.7-3 mm wide, dry, indurated, scarious and minutely ciliolate along the margins, appressed-hirtellous; petals elliptic to subobovate, acute and reflexed, 5 mm long and 1.8-2 mm wide, yellowish-white, appressed-hirtellous along the midline; stamens 3.5-4 mm long, the filaments free, ca 0.8-1 mm long, without dorsal appendages; anthers ca 1.5 mm long, unappendaged (sometimes 1-mucronate at the apex?), dorsally sparsely appressed-hirtellous, the connectives dilated from the base into oblong-ovate scales, these brownish, narrowed to an obtuse or acute apex, entire or obscurely erosulose below, exceeding the anthers by 1.2-1.5 mm; ovary ovoid, appressed-rufous-hirtellous, the placentae 3-ovulate; style ca 2.6-2.8 mm long, appressed-rufous-hirtellous on the lower half. *Capsule* ovoid, 3-lobate, narrowed at the base, apiculate at the apex, up to 2.5 cm

long, the valves cymbiform, the pericarp reticulate, puberulous; seeds ca 4.5 mm long, densely puberulous.

Costa Rica, Panama, and Colombia; wet forests.

CANAL ZONE: Barro Colorado I, *Standley 31414* (US), *41019* (US), *Wilson 84* (F), *89* (F); Gamboa, *Standley 28384* (US); 2 mi S of Gamboa, Quebrada de Oro, *Wheeler & Zetek s.n.* (US); Obispo, *Standley 31675* (US); Las Cruces Trail nr George Green Memorial, *Dwyer 5600* (MO); Río Paraíso, above E Paraíso, *Standley 29909* (US); along Caño Quebrado, *Pittier 6665* (US). DARIEN: NW of Yaviza, *Duke 6536* (MO); Cerro Pidiaque, *Duke 8077* (MO). PANAMA: Sabanas N of Panama City, *Bro. Paul 460* (F); Río Tapía, *Standley 28248* (US); Río Indio, Madden Lake (Canal Zone?), *Miller 2051* (US), *2052* (MO, US); along Pan-Amer Hwy ca halfway betw El Llano & Río Mamoní, *Duke 5634* (MO).

I have not seen the type specimen *Seemann 548* (nr Cruces, in dark forests).

2. **Rinorea squamata** Blake, Contr. U. S. Nat. Herb. **20:** 516, 1924.—Fig. 1(A-F).

Shrub or small tree, 2.5-6 (12) m high, the trunk to 6.5 (20) cm in diam, the branchlets ferruginous-puberulous and sparsely hirsute. *Leaves* opposite, the petioles up to 8 mm long, puberulous and sparsely hirsute; blade usually slightly oblique, narrowly obovate-elliptic to obovate-elliptic, or narrowly elliptic, acute to obtuse at the base, rather abruptly long-acuminate at the apex, crenulate to serrulate to subentire at the margins, up to 13 cm long and 5 cm wide, chartaceous, puberulous and sparsely hirsute especially along the prominent midvein below. *Racemes* terminal, up to 6 cm long, the rhachis ferruginous-puberulous. *Flowers* with the pedicels up to 2.5 mm long, minutely ferruginous-puberulous, the bracteoles broadly ovate, ca 0.8 mm long, minutely ciliolate, ferruginous-puberulous especially along the thickened midvein; sepals subequal, broadly to very broadly ovate, acute to subobtuse, 1.1-1.6 mm long and 1.1-1.3 mm wide, minutely ciliolate, ferruginous-puberulous especially along the midvein; petals ± oblong, obtuse and reflexed, 4-4.5 mm long and 1.1-1.3 mm wide, whitish or yellowish, minutely ciliolate; stamens 2.8-3 mm long, the filaments free, large, ca 1 mm long, the dorsal appendages oblong, about as long as or slightly shorter than the filaments, about as wide as the latter, free from near the middle; anthers 1-1.2 mm long, unappendaged, the connective dilated from the base into brownish, ovate, obtuse to ± acute, basally erosulose scales exceeding the anthers by ca 1-1.2 mm; ovary subglobose, densely hispid-pilose, the placentae 1-ovulate; style ca 2.5 mm long, glabrous. *Capsule* ovoid, 3-lobulate, narrowed at the base, acuminate-mucronate at the apex, ca 2 cm long, the valves cymbiform, the pericarp coriaceous, slightly reticulate, hirsute-hispid; seeds ca 6 mm long, glabrous.

Costa Rica and Panama; known in Panama as *guayacillo* (fide *Cooper & Slater 44*) or *molenillo* (fide *Standley 28037*).

BOCAS DEL TORO: Daytonia Farm, Region of Almirante, *Cooper 400* (F, MO, US); Almirante Region, *Cooper & Slater 44* (US); Changuinola Valley, *Dunlap 564* (F, US); Fish Creek Mts, vic of Chiriquí Lagoon, *von Wedel 2221* (MO, US), *2298* (MO, US), 2322 (MO, US). CANAL ZONE: Chagres River, 2-3 mi of mouth, *Stevens 1296* (US); nr Gatun, *Goldman 1864* (holotype US); forest betw Peluca Hydrographic Station & Quebrada

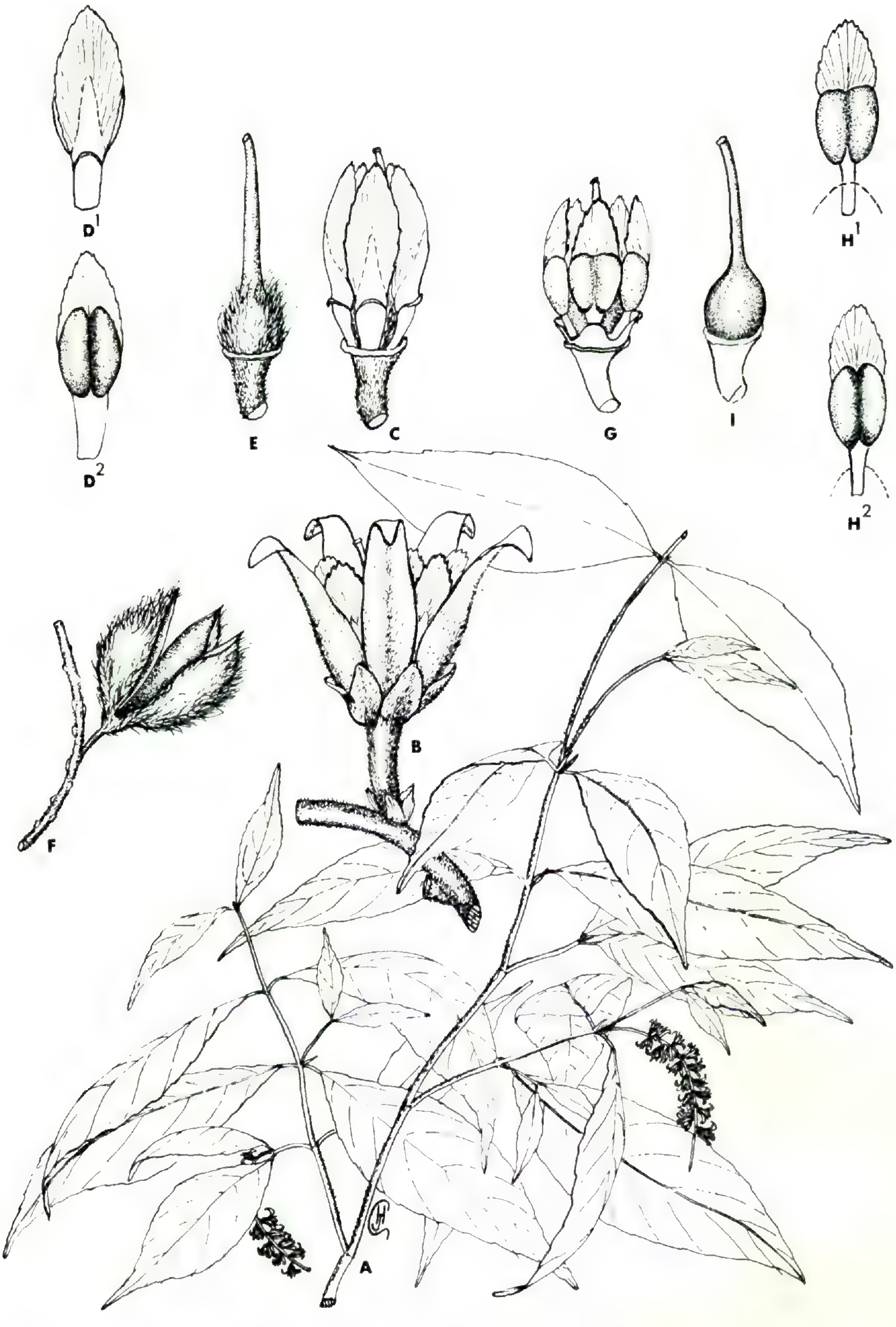

Fig. 1. *Rinorea squamata* Blake: A, habit (×½); B, flower (×6); C, id., calyx and corolla removed (×7); D^1, stamen, abaxial view (×8); D^2, id., adaxial view (×8); E, pistil (×8); F, dehiscing capsule (×1). A-E after *Bro. Paul 442* (US); F after *Dunlap 654* (US). *R. roureoides* Woodson: G, flower, calyx and corolla removed (×7); H^1, stamen, abaxial view (×8); H^2, id., adaxial view (×8); I, pistil (×8). After *Allen 4099* (MO).

Peluca, along Río Boqueron, *Steyermark & Allen 17225* (MO). DARIEN: Caná-Cuasi trail (Camp 2), Chepigana Distr, alt 2000 ft, *Terry & Terry 1430* (F, MO); Río Chucunaque, betw Río Membrillo & Río Subcuti, *Duke 8590* (MO); woodlands & pasture margins nr El Real, *Stern et al. 781* (MO, US); 2-3 mi SE of El Real, *Duke 4857* (MO); trail betw Pinogana & Yavisa, alt ca 15 m, *Allen 247* (F, MO, US); rd to Río Tucuti, on ridge upstream above Tucuti, *Duke 5269* (MO); shores of a small river, Ensenada Guayabo betw Punta Guayabo Grande & Punta Guayabo Chiquita, *Stern & Chambers 183* (MO, US); Cocalita, *Dwyer 4453* (MO); bank above Río Paca, *Stern et al. 586* (MO, US). PANAMA: Sabanas N of Panama City, *Bro. Paul 442* (F, US); Río Tapía, wet forest, *Standley 26141* (US), *26150* (US), *28037* (US), *28245* (US), *41187* (US).

3. **Rinorea brachythrix** Blake, Contr. U. S. Nat. Herb. **20:** 510, *pl. 34*, 1924.

Shrub, the branchlets sparsely hirtellous or glabrous. *Leaves* opposite, the petiole flattened and subcanaliculate above, 7-14 mm long, minutely hirtellous; blade slightly inequilateral or not, narrowly ovate, acute to obtuse at the base, acuminate at the apex, remotely serrulate with black, gland-tipped teeth at the margins, 11.5-17 cm long and 4-5.5 cm wide, rigid-chartaceous, minutely hirtellous along the midvein to glabrous above, sparsely strigose along the prominent midvein to glabrous beneath. *Racemes* terminal, up to 4 cm long, the rhachis densely hirtellous. *Flowers* with the pedicels 3-4 mm long, articulate below the middle, densely hirtellous, the bracteoles triangular-ovate, acute, carinate dorsally, ca 1.5 mm long, ciliolate, hirtellous to hirsute along the carina; sepals subequal, broadly ovate, acute, 2-2.5 mm long and 1.6-2 mm wide, ciliolate, appressed-hirtellous especially towards the apex; petals ovate to narrowly ovate, obtuse and reflexed, ca 5 mm long and 1.8-2.2 mm wide, yellow, sparsely ciliolate towards the base; stamens 3.8-4 mm long, the filaments free, very short, scarcely 0.4 mm long, the dorsal appendages about as long as the filaments; anthers ca 2 mm long, each theca mucronate, the connectives dilated from the base into brownish, ovate, obtuse, obscurely erosulose scales exceeding the anthers by ca 1.5 mm; ovary ovoid, densely strigillose, the placentae 2-ovulate, the style ca 2.8 mm long, strigillose below. *Capsule* (immature) ellipsoid-globose, apiculate, densely strigillose, the seeds sparsely short-hirsute.

Native to Panama.

DARIEN: vic of La Palma, alt 0-50 m, on hills, *Pittier 6601* (holotype US).

4. **Rinorea roureoides** Woodson, Ann. Missouri Bot. Gard. **37:** 403, 1950.—Fig. 1(G-I).

Tree 7 m tall, the branchlets inconspicuously puberulous. *Leaves* alternate, the petiole canaliculate above, 4-7 mm long, glabrous; blade narrowly elliptic to narrowly obovate or obovate, obtuse to rounded at the base, usually bluntly long-acuminate at the apex, remotely repand-serrulate at the margins, 7-12.5 cm long and 2.2-4.7 cm wide, rigid-chartaceous, glabrous, ± lustrous above, dull and with the venation prominent beneath. *Inflorescences* lateral and terminal, paniculate, the panicles solitary or few-fasciculate, the rhachis and peduncles minutely puberulous. *Flowers* with the pedicels 2-3 mm long, articulate below the middle, minutely puberulous, the bracteoles ca 0.5 mm long, minutely ciliolate and puberulous;

sepals subequal, subcircular, ca 1-1.3 mm long and 1 mm wide, membranous, finely ciliolate, persistent; petals oblong-subobovate, ± rounded at the apex, ca 3 mm long and 1.4 mm wide, white, finely ciliolate; stamens ca 2.5 mm long, the filaments ca 0.8 mm long, the dorsal appendages ca 0.5 mm long, connate into a low tube, the tube sinuate at the apex and with the upper margin free; anthers about as long as the filaments, unappendaged, short-pilose dorsally, the connectives dilated apically into brownish, broadly ovate, erose scales exceeding the anthers by 0.5-0.8 mm; ovary subglobose, ca 1 mm long, glabrous, the placentae 1-ovulate, the style ca 1.5-2 mm long. *Capsule* obovoid-globose, acute, ca 5-6 mm long, glabrous.

Native to Panama.

COLÓN: Río Viejo, vic of Puerto Pilon, alt 10 m, *Allen 4099* (holotype MO).

5. **Rinorea blakeana** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 349, 1940.

Shrub 2-3 m high, the branchlets slender, minutely puberulous. *Leaves* alternate (distichous?), the petiole canaliculate above, 2.5-5 mm long, minutely puberulous; blade narrowly ovate, ± acute to obtuse at the base, gradually and bluntly long-acuminate at the apex, entire-margined or almost so, up to 11 cm long and 3 cm wide, membranous-chartaceous, glabrous or almost so on both sides, very slightly discolor, the lower surface slightly paler. *Inflorescences* axillary, few-flowered, contracted-racemose (or of contracted cincinni?). *Flowers* with the pedicels up to 5 mm long, articulate below the middle, minutely puberulous, the bracteoles ca 1 mm long, finely ciliolate and minutely puberulous; sepals slightly unequal, subcircular, rounded at the apex, 1.2-1.8 mm long, membranous, finely ciliolate, nearly glabrous, persistent; petals up to 5 mm long, white, glabrous; stamens ca 2.8-3 mm long, the filaments 0.7-1 mm long, the dorsal appendages obovate, free at the apex, about as long as the filaments, slightly wider than the latter at the apex, free from each other (or perhaps united at the base into a very low tube?); anthers ca 0.8-1 mm long, unappendaged, the connectives dilated apically into whitish, narrowly ovate-oblong scales, these incised (usually 3-dentate) at the apex and exceeding the anthers by ca 1.5 mm; ovary glabrous, the placentae 2-3-ovulate (?), the style gradually narrowed towards the apex. *Fruit* unknown.

Native to Panama.

DARIEN: Caná-Cuasi trail, Chepigana Distr, alt 5000 ft, *Terry & Terry 1513* (holotype F, isotype MO).

The systematic position of this species is uncertain. The alternate, probably distichous leaves and the contracted racemose inflorescences (or contracted cincinni) suggest the genus *Gloeospermum* Triana & Planchon, but, lacking fruits, I am reluctant to make the transfer.

2. GLOEOSPERMUM

Gloeospermum Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **17:** 128, 1862.

Shrubs or trees. *Leaves* alternate, distichous, the petiole short, the stipules small and deciduous, the blade entire to serrate. *Flowers* in axillary, compact, mostly few-flowered, bracteate cymes, small, actinomorphic, mucilaginous; pedicel articulate; sepals free, equal or mostly unequal, persistent; petals imbricate, free, equal or nearly so, sessile, agglutinated in bud, white, yellow or reddish, deciduous with the stamens; filaments flattened, with dorsal, erect, carnose, glandular appendages, these mostly free at the apex and united into a tube equalling or shorter than the filaments; anthers free, with apical connective scales about as long as or twice as long as the anthers; ovary with 3 placentae, each bearing few, 2-seriate ovules; style ± subulate, the stigma terminal and punctiform. *Fruits* baccate, indehiscent, the pericarp carnose and mucilaginous; seeds few, the endosperm carnose, the cotyledons large and foliaceous.

A small, neotropical genus represented in Panama by two species; two additional species occur in Central America (cf. A. Robyns, Ann. Missouri Bot. Gard. **53:** 110-112, 1966).

a. Leaves and calyx densely ferruginous-punctate; outer sepals ca 1.8 mm in diam, the inner ones ca 2.5 mm in diam ..... 1. *G. ferrugineostictum*

aa. Leaves and calyx epunctate; outer sepals ca 1.5 mm in diam, the inner ones ca 1.8 in diam ..... 2. *G. portobelense*

1. **Gloeospermum ferrugineostictum** A. Robyns, Ann. Missouri Bot. Gard. **53:** 111, 1966.

Tree ca 4 m high, the branchlets terete, glabrous, green with numerous, elongate, ferruginous puncta. *Leaves* glabrous, the pedicel thick, subcanaliculate above, up to 1 cm long; blade narrowly elliptic, acute at the base, bluntly long-acuminate at the apex, entire-margined or the margins subcrenulate above the middle, up to 20 cm long and 7 cm wide, rigid-chartaceous, discolor when dry, the lower surface darker, the venation prominent especially beneath, densely ferruginous-punctate especially beneath, the puncta elongate on the veins. *Inflorescences* at first dichasial, the lateral shoots developing into cincinni, the bracts inconspicuously puberulous and ciliolate. *Flowers* with the (fruiting) pedicel up to 5 mm long, articulate 2 mm above the base, inconspicuously puberulous and densely ferruginous-punctate; buds ovoid; sepals subcircular, rounded to obtuse, inconspicuously puberulous and ciliolate, densely ferruginous-punctate, unequal, the 2 outer ones ca 1.8 mm in diam, the 2 inner ones ca 2.5 mm in diam; petals (immature) ovate, obtuse, ca 3.5 mm long, yellow, ferruginous-punctate above; androecium less than 3 mm long, the dorsal appendages of the filaments connate into a tube less than 0.5 mm long, the upper margin of the tube free, the anthers ca 1 mm long, the connective scales thin-scarious, ± elliptic, obtuse to acute, slightly unequal, up to 1.5 mm long and 0.5 mm wide; ovary glabrous. *Fruit* baccate, surmounted by the

persistent style, ca 8 mm in diam (ca 12.5 mm long, when fresh, according to note on type specimen), green when fresh, gray when dry, glabrous.

Native to Panama.

BOCAS DEL TORO: s. loc., *von Wedel 445* (holotype MO, isotype F).

2. **Gloeospermum portobelense** A. Robyns, Ann. Missouri Bot. Gard. **53:** 111, 1966.

Tree 4 m high, entirely glabrous. *Leaves* with petioles slightly canaliculate above, 3-6 mm long, the stipules narrowly ovate-triangular, 6 mm long and 1.5 mm wide; blade narrowly elliptic, rounded at the base, acuminate at the apex, entire-margined, up to 13.5 cm long and 4.7 cm wide, rigid-chartaceous, the venation prominent especially beneath. *Inflorescences* of few-flowered cincinni. *Flowers* with the pedicels up to 5 mm long, articulate 1 mm above the base; buds ovoid, ca 5 mm long; sepals broadly ovate to very broadly ovate, obtuse, inconspicuously ciliolate, unequal, the 2 outer ones ca 1.5 mm in diam, the 2 inner ones ca 1.8 mm in diam; petals ovate, obtuse, ca 5.5 mm long and 2.5 mm wide, white; androecium ca 3.8-4 mm long, the dorsal appendages of the filaments connate into a tube ca 0.7-0.8 mm long, irregularly lobed and with the upper margin free, the anthers ca 1 mm long, the thecae slightly divergent at the base, the connective scales thin-scarious, oblong-ovate, obtuse, entire to inconspicuously erosulose, unequal, ca 2-2.5 mm long and 0.5-0.6 mm wide; ovary ca 1 mm long, the style ca 4 mm long, gradually narrowed towards the apex. *Fruit* unknown.

Native to Panama.

COLÓN: Portobelo, Las Cruces Trail, *Ebinger 116* (holotype US, isotype MO).

3. AMPHIRRHOX

Amphirrhox Spreng. in L., Syst. Veg. ed. 16, **4**(2): 51, 99, 1827.

Shrubs or trees, glabrous. *Leaves* alternate or subopposite, often grouped towards the apex of the branchlets, the petioles short, the stipules small and deciduous, the blade often repand-serrate. *Inflorescences* of long-pedunculate cymes, these few-fasciculate laterally or at the apex of the branchlets. *Flowers* slightly zygomorphic, the pedicels articulate; sepals unequal, the 2 outer ones 1/2-1/3 smaller than the 2 inner ones; petals free, unguiculate, the anterior petal ca twice as broad as the others and usually emarginate at the apex, white, yellowish, lilac or blue; filaments bearing dorsal, erect, carnose, glandular appendages united into a low tube, the connective scales ± long and scarious; ovary with 3 placentae, the ovules numerous, the style filiform, erect, the stigma somewhat enlarged, truncate and inconspicuously denticulate. *Capsules* 3-valvate, the valves cymbiform, the lignous-cartilaginous endocarp separating from the exocarp; seeds with the testa coriaceous, the endosperm carnose.

A small, neotropical genus with only one species in Panama.

1. **Amphirrhox longifolia** (St.-Hil.) Spreng. in L., Syst. Veg. ed. 16, **4**(2): 99, 1827.

Spathularia longifolia St.-Hil., Hist. Pl. Remarqu. Brés. Parag. 318, *t.* 28, 1825.
Amphirrhox latifolia Mart. ex Eichl. in Mart., Fl. Bras. **13**(1): 376, 1871.

Shrub or small tree up to 11 m tall, the trunk up to 12.5 cm in diam. *Leaves* with the petioles canaliculate above, up to 12 mm long or more; blade narrowly elliptic to narrowly elliptic-subobovate, acute and narrowly decurrent at the base, acuminate at the apex, remotely serrulate to serrate at the margins, 5.5-16 cm long and 1.7-6 cm broad, chartaceous, the midvein prominent and the lateral veins prominulous beneath. *Inflorescences* axillary and terminal, of few-fasciculate, mostly 3-flowered cymes, the peduncles up to 6 cm long. *Flowers* with the pedicels up to 1 cm long, articulate below the middle; sepals ovate to broadly ovate, obtuse to ± rounded, the 2 outer ones ca 2.5-3 mm long, the 2 inner ones ca 4.5-5 mm long; petals white or creamy white, up to 2 cm long, the anterior petal oblong-obcordate and up to 6 mm wide, the other petals oblong, slightly falcate, obtuse, up to 3.5 mm wide; filaments ca 1-1.5 mm long, the dorsal appendages united into a tube ca 1/2 as long as the filaments; anthers ca 1-1.5 mm long, the connective scales oblong to linear, obtuse, ca 1/2 as long as to equalling the anthers; ovary ovoid, 3-sublobulate, ca 1-1.5 mm long, the style up to 4 mm long. *Capsule* ellipsoid, 3-lobate, up to 2.4 cm long, the pericarp green when fresh and muricate; seeds up to 8 mm long, the testa blackish-brown and shining.

Panama, Colombia, Venezuela, the Guianas, Brazil, and Peru.

BOCAS DEL TORO: region of Almirante, Buena Vista Camp on Chiriquí trail, alt 375 m, *Cooper 605* (F, US); Fish Creek, vic of Chiriquí Lagoon, *von Wedel 2201* (MO, US), *2227* (MO, US).

This species was first reported in Panama and in North America by Standley in 1929 (Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 236).

According to Melchior (in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, **21:** 356, 1925), *A. longifolia* and *A. latifolia* can be separated by the length of the connective scales: in the first species the scales are about as long as the anthers, while in the latter they more or less equal the anthers. Among the three Panamanian collections, I might then distinguish two species, von Wedel's collections being *A. longifolia* and the Cooper collection *A. latifolia.* Since, however, the other floral and vegetative characters seem to be identical in both species, I consider, with Smith & Fernández-Pérez (Caldasia **6:** 120, 1954), *A. latifolia* a synonym of *A. longifolia.* More collections are needed for an evaluation of the scale character.

4. HYBANTHUS

Hybanthus Jacq., Enum. Syst. Pl. Ins. Carib. 2, 17, 1760.

Herbs, suffrutices, shrubs, or infrequently small trees. *Leaves* alternate, sometimes opposite, petiolate or sessile, the stipules usually small and persistent, rarely caducous, the blade entire-margined or ± serrate or crenate. *Flowers* usually

axillary and solitary or few-fasciculate, sometimes in axillary or terminal racemes, rarely in cymose inflorescences, zygomorphic; pedicels articulate; sepals free, subequal, without basal auricles, persistent; petals unequal, persistent or not; anterior petal smaller or mostly much larger than the others, unguiculate, the claw gibbous-saccate or shortly calcarate at the base; stamens with the anthers subsessile or on distinct filaments, these free or connate, the 2 anterior ones each bearing a nectariferous appendage dorsally, the appendages free or coherent; anthers free or coherent, with membranous connective appendages apically; ovary with 3 placentae, each placenta (2-) 3-∞-ovulate; style usually clavate, the apex slightly curved to uncinate, the stigma terminal. *Capsules* loculicidally and elastically 3-valvate, the valves carinate; seeds globose or ovoid, the testa smooth or alveolate, the endosperm copious, the cotyledons flat.

A genus of about 100 species distributed throughout the tropics, but most abundant in tropical America; three species at present reported from Panama.

Useful references are:

Schulze, G. K., Morphologisch-systematische Studien über die Gattung *Hybanthus* mit besonderer Berücksichtigung der südamerikanischen Arten. Engl. Bot. Jahrb. **67:** 437-492, 1936.

Morton, C. V., The genus *Hybanthus* in continental North America. Contr. U. S. Nat. Herb. **29:** 74-82, 1944.

a. Shrubs, infrequently small trees; anterior petal up to 4 cm long; capsule up to 2 cm long; seeds 4-5 mm long .....1. *H. prunifolius*

aa. Herbs, annual or perennial; anterior petal up to 11 mm long; capsule up to 5 mm long; seeds 1.5-1.8 mm long.

b. Annual herbs; leaves, at least the lower ones, opposite or subopposite; anterior petal 8-10 mm long; anterior filaments with subglobose glands dorsally; capsule up to 5 mm long; seeds ca 1.8 mm long .....2. *H. attenuatus*

bb. Perennial herbs; leaves alternate; anterior petal up to 11 mm long; anterior filaments calcarate dorsally, the spur ca 0.5 mm long; capsule ca 4 mm long; seeds ca 1.5 mm long .....3. *H. thiemei*

1. **Hybanthus prunifolius** (Schult.) Schulze, Notizbl. Bot. Gart. Mus. Berlin **12:** 114, 1934.

Viola prunifolia Schult. in Roem. & Schult. in L., Syst. Veg. ed. nov., **5:** 391, 1819.
Ionidium anomalum H. B. K., Nov. Gen. Sp. Pl. **5:** 381, *t. 500*, 1821.
Hybanthus anomalus (H. B. K.) Melchior in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, **21:** 359, 1925.

Shrub, infrequently small tree, 1-7 m high, the branchlets whitish, puberulous when young. *Leaves* alternate, the petiole up to 7 mm long, ± canaliculate above, puberulous, the stipules ovate, concave, acuminate, ca 3 mm long, cartilaginous, whitish, persistent; blade narrowly elliptic to elliptic, obtuse to usually acute at the base, long-acuminate at the apex, serrulate to crenulate at the margins, up to 15 cm long and 6 cm wide, membranous-chartaceous, sparsely cinereous-pubescent especially along the midvein on the lower surface, becoming glabrescent. *Flowers* axillary, solitary, the pedicel slender, articulate above the middle, up to 1.7 cm

long, puberulous, the bracteoles inserted towards the base of the pedicel, broadly ovate, acute, ca 3-3.5 mm long and wide, cartilaginous, whitish, puberulous and persistent; sepals triangular-ovate, obtuse to acute, ca 9 mm long and 4-4.5 mm wide, puberulous outside; petals white, finely puberulous outside; anterior petal up to 4 cm long, the claw geniculate-calcarate, the blade ovate, rounded at the apex, ca 2.7 cm long and 1.8 cm wide; lateral petals oblique-oblong, rounded at the apex, ca 17 mm long and 5-5.5 mm wide; posterior petals ± oblong, subacute, ca 10 mm long and 4.5 mm wide; filaments very short, the 2 anterior ones calcarate, the spur recurved at the apex, ca 2.5 mm long and puberulous; anthers coherent, ca 3.5 mm long, the connective appendages ca 2.5 mm long and brownish; ovary ovoid-ellipsoid, ca 4 mm long, glabrous (or sometimes sparsely pilose?), the style ca 5 mm long, slightly tapering towards the curved apex. *Capsule* ellipsoid, 3-gonous, acute, up to 2 cm long, the seeds ovoid, 4-5 mm long.

Costa Rica, Panama, Colombia, and Venezuela; wet forest.

CANAL ZONE: Bejuco railway-station, *Hayes* 33 (US); Barro Colorado I, *Frost 193* (F), *200* (F), *Netting 61* (F), *Shattuck 868* (F, US), *Standley 31261* (US), *31317* (US), *40795* (US), *Woodworth & Vestal 387* (F), *591* (F); hills N of Frijoles, *Standley 27462* (US). COCLÉ: mts beyond La Pintada, alt 400-600 m, *Hunter & Allen 646* (F, MO, US). DARIEN: Caná & vic, alt 2000-6500 ft, *Williams 780* (US); Paca, *Williams 781* (US); vic of Pinogana, *Pittier 6530* (US); Río Sabana, *King Léopold III 124* (MO).

2. **Hybanthus attenuatus** (Schult.) Schulze, Notizbl. Bot. Gart. Mus. Berlin **12:** 114, 1934.

Ionidium attenuatum Schult. in Roem. & Schult. in L., Syst. Veg. ed. nov., **5:** 402, 1819.
I. riparium H. B. K., Nov. Gen. Sp. Pl. **5:** 378, 1821.
Hybanthus riparius (H. B. K.) Standley in Standley & Cald., List. Prel. Pl. Salvador 152, 1925.

Herb, annual, erect, to 30 cm high or more, simple to much-branched, the lower branches opposite to subopposite, puberulous, the hairs simple and mostly curved upwards. *Leaves*, at least the lower ones, opposite or subopposite, the petioles 3-7 mm long, puberulous, the stipules narrowly ovate, ciliolate, ca 1.5 mm long, persistent; blade narrowly ovate, attenuate-decurrent at the base, acuminate at the apex, serrate to serrulate-crenulate at the margins, up to 8 cm long and 3 cm wide, membranous, sparsely and minutely puberulous especially along the veins and the margins, to glabrescent. *Flowers* axillary, solitary, the pedicels filiform, elongated, articulate above the middle, up to 2 cm long, puberulous, the bracteoles triangular-ovate, slightly carinate, acute, ca 1 mm long or less, ciliolate; sepals triangular-ovate, slightly carinate, acuminate, 2.5-4 mm long and 0.7-0.8 mm wide, puberulous outside and ciliolate; petals white with purple stripes; anterior petal 8-10 mm long, the claw gibbous-saccate and pubescent inside, the blade broadly angular-elliptic and obtuse to rounded at the apex; lateral petals ca 1/2 as long as the anterior one, inequilateral, ± falcate; posterior petals narrowly oblong, ca 2.5-3 mm long; filaments very short, the 2 anterior ones with a subglobose gland dorsally; anthers ca 1.3 mm long, the 2 anterior ones dorsally puberulous, the connective appendages broad, obtuse to rounded at the apex, ca 0.8-1.2 mm long; ovary pyriform, ca 1 mm long, glabrous, the style ca 1.8 mm long, enlarged towards

Fig. 2. *Hybanthus thiemei* (J. D. Sm.) Morton: A, habit (×½); B, flower (×4); C, id., calyx removed (×4); D¹, petal, adaxial view (×4); D², id., ¾ lateral view (×4); E, flower, calyx and corolla removed (×8); F¹, stamen, adaxial view (×8); F², id., lateral view (×8); G, pistil (×8); H, capsule surrounded by persistent calyx and corolla (×4); I, seed (×4). After *Alston & Allen 1859* (MO).

the curved apex. *Capsule* ellipsoid, acute, up to 5 mm long, glabrous, the seeds subglobose, ca 1.8 mm long, the testa finely alveolate.

Arizona, U.S.A., Mexico, Central America, and South America to Peru.

According to Standley (under *H. riparius*) (Contr. U. S. Nat. Herb. **27:** 271, 1928), *H. attenuatus* is frequent on the Pacific slope in Panama.

CANAL ZONE: vic of Miraflores Lake, *White & White 196* (MO, US); Camino de Corozal, *Bro. Heriberto 245* (US); Hospital Grounds at Ancon, alt 20-30 m, *Pittier 2755* (US); Sosa Hill, Balboa, brushy slope, *Standley 25287* (US), *26457* (US). PANAMA: Sabanas N of Panama City, *Bro. Paul 487* (US); La Exposición, *Bro. Heriberto 244* (US); Taboga I, *Pittier 3561* (US); id., moist thicket, *Standley 27035* (US); id., brushy slope, *Standley 27980* (US).

3. **Hybanthus thiemei** (J. D. Sm.) Morton, Contr. U. S. Nat Herb. **29:** 81, 1944. —Fig. 2.

Ionidium thiemei J. D. Sm., Bot. Gaz. **40:** 1, 1905.

Herb, perennial, usually erect, up to 18 cm high, simple or sparsely branched, the stems puberulous, the hairs simple and curved upwards. *Leaves* alternate, the petioles slender, up to 6 mm long (up to 3 cm long in collections from Honduras), densely puberulous with the hairs curved upwards, the stipules subulate, ca 2 mm long, puberulous, persistent, blade ovate, attenuate-cuneate at the base, obtuse at the apex, serrulate-crenulate at the margins, up to 4.7 cm long and 2.3 cm wide, membranous, sparsely pilose especially on the lower surface, the hairs ± straight but curved upwards along the midvein. *Flowers* axillary, solitary, the pedicels filiform, elongated, articulate close to the apex, up to 3 cm long, puberulous with the hairs curved upwards; sepals ovate or triangular-ovate, acute, 3-4 mm long and 1-1.8 mm wide, puberulous outside; petals white; anterior petal up to 11 mm long, the claw gibbous-saccate, the blade broadly elliptic-ovate, rounded at the apex, ca 6 mm long and 5 mm wide, minutely puberulous along the veins; lateral petals oblique-oblong, ca 4.5 mm long and 1.5 mm wide; posterior petals oblong-obovate, ca 2.5 mm long and 1 mm wide; filaments ca 0.5 mm long, united into a low ring, the 2 anterior ones calcarate dorsally, the spur curved and ca 0.5 mm long; anthers ca 1 mm long, the 2 anterior ones dorsally pilose, the connective appendages broad, rounded at the apex and ca 0.5 mm long; ovary globose, ca 1 mm long, glabrous, the style ca 1.5 mm long, thickened toward the unciform apex. *Capsule* ellipsoid, mucronate, ca 4 mm long, glabrous, the seeds pyriform, ca 1.5 mm long, the testa minutely alveolate.

Southern Mexico to Panama.

COCLÉ: N rim of El Valle, *Alston & Allen 1859* (F, MO, US).

5. CORYNOSTYLIS

Corynostylis Mart. in Mart. & Zucc., Nov. Gen. Sp. Pl. **1:** 25, 1823.

Lianas or scandent shrubs. *Leaves* alternate, petiolate, the stipules early caducous, the blade entire-margined to serrate-margined. *Inflorescences* axillary or

terminal, racemose, or flowers axillary and solitary. *Flowers* large, zygomorphic, often resupinate; pedicels elongated, filiform, articulate, 2-bracteolate; sepals free, subequal, without basal auricles, deciduous; petals strongly unequal, deciduous, the anterior petal long-calcarate, the spur cylindrical; filaments very short, flattened, united; 2 anterior filaments dorsally calcarate, the spurs united and villous; 2 lateral filaments each with a short, dorsal, villous, nectariferous appendage; anthers coherent, the connectives produced apically into membranous appendages; ovary with 3 placentae, the ovules ∞, in multiple rows, the style clavate, the stigma circular, anterior, slightly immersed in the style apex. *Capsules* large, lignous, loculicidally 3-valvate, the valves not elastic; seeds numerous, almost 4-gonous, strongly compressed, the testa crustaceous and rugose; endosperm scant; cotyledons foliaceous.

A neotropical genus of three or four species; the following is the only one in Panama and Central America.

1. **Corynostylis arborea** (L.) Blake, Contr. U. S. Nat. Herb. **23:** 837, 1923.

Viola arborea L., Syst. Nat. ed. 10, 1239, 1759.
V. hybanthus L., Sp. Pl. ed. 2, 1328, 1763.
Corynostylis hybanthus (L.) Mart. in Mart. & Zucc., Nov. Gen. Sp. Pl. **1:** 26, *t. 17-18,* 1823.

Vine, lignous, the young branchlets ferruginous-puberulous. *Leaves* with the petioles canaliculate above, up to 7 mm long, glabrescent, the stipules small, subulate; blade ovate or ovate-elliptic, acute to rounded at the base, ± abruptly and shortly acuminate at the apex, subentire-margined, 3.5-9 cm long and 1.5-5 cm wide, rigid-chartaceous, glabrous, the midvein and lateral veins prominent below. *Flowers* axillary, solitary but grouped towards the apex of the branchlets, or in terminal or lateral racemes; pedicel articulate above the middle, up to 5 cm long, sparsely puberulous below, the bracteoles inserted ± medially on the pedicel, ovate, obtuse to acute, up to 1.5 mm long, ciliolate; sepals broadly ovate, rounded to obtuse, 2.5-3.5 mm long and 2.2-2.5 mm wide, subcarnose towards the base, minutely and finely ciliolate; petals white or pinkish-white, minutely and finely ciliolate; anterior petal 2.8-4.2 cm long (spur included), the blade broadly ovate to subcircular, 1-1.4 cm in diam, the spur obtuse at the base, slightly twisted, 2-2.8 cm long; lateral petals oblique-obovate, rounded at the apex, 11-16 mm long and 7-11 mm wide; posterior petals obovate, slightly oblique, rounded at the apex, 6-7.5 mm long and 4-5.5 mm wide; anterior filaments with the united spurs 2-3.5 mm long; anthers ca 4 mm long, the connective appendages rounded at the apex, 1.5-2.5 mm long; ovary subglobose, ca 2.8-3 mm long and 2-2.5 mm wide, sparsely pilose on the upper part, the style 5.5-6 mm long, geniculate above the base, the apex slightly curved. *Capsule* ovoid-ellipsoid, up to 5.5 cm long and 3.5 cm broad, glabrous; seeds with irregular margins, 1-1.5 cm in diam, the testa brownish on one side, grayish on the other side.

Throughout tropical America.

CANAL ZONE: nr Gatun, *Hayes 13* (US); along Trinidad River, nr sea level, *Pittier 3972* (US). DARIEN: betw Río Membrillo & Río Subcuti, *Duke 8598* (MO).

According to Standley (Contr. U. S. Nat. Herb. **27:** 271, 1928), *C. arborea* is "occasional in forests on the Atlantic slope."

6. VIOLA

Viola L., Sp. Pl. 933, 1753; Gen. Pl. ed. 5, 402, 1754.

Herbs, annual or perennial, rarely suffrutices, often acaulescent. *Leaves* alternate, petiolate, the stipules sometimes foliaceous, persistent. *Flowers* axillary, usually solitary, zygomorphic, often dimorphous (cleistogamous flowers following chasmogamous ones); pedicels not articulated; sepals subequal, usually basally auricled; petals spreading, unequal, the anterior petal the largest and basally calcarate; filaments very short, free; anthers free or mostly connivent into a sheath around the ovary, the 2 anterior ones with spur-like or wart-like, nectariferous appendages at the base, these extending into the spur of the anterior petal, the connectives produced apically into conspicuous, membranous appendages; ovary with 3 ∞-ovulate placentae; style almost erect or usually ± curved downwards, ± thickened or sometimes gradually tapering towards the apex, entire or variously appendaged, the style apex and stigma variously shaped. *Capsules* loculicidally and elastically 3-valvate, the valves carinate and dorsally thickened; seeds globose-ovoid, arillate or not, usually smooth; endosperm abundant; embryo straight; cotyledons rather thick, plano-convex.

A cosmopolitan genus of about 400 species distributed chiefly in temperate regions of the northern hemisphere; restricted to mountain regions in the tropics; one of the four species reported from Panama is introduced.

a. Acaulescent plants.
   b. Sepals 4.5-5.5 mm long, the basal auricles ca 1 mm long; anterior petal 13 mm long, the spur scarcely 2 mm long ..... 1. *V. guatemalensis*
   bb. Sepals ca 10 mm long, the basal auricles ca 3 mm long; anterior petal 15 mm long, the spur ca 4 mm long ..... 2. *V. odorata*

aa. Herbs with creeping, climbing or ± erect stems.
   c. Stems ± erect; stipules up to 2 cm long; leaf blade oblique, narrowly elliptic, cuneate at the base; pedicel up to 6 cm long; connective appendages ca 1 mm long ..... 3. *V. stipularis*
   cc. Stems creeping or climbing; stipules up to 5 mm long; leaf blade triangular-ovate, cordate at the base; pedicel up to 2.5 cm long; connective appendages ca 1.5-1.8 mm long ..... 4. *V. scandens*

1. **Viola guatemalensis** Becker, Repert. Sp. Nov. **20:** 6, 1924 [§ *Nomimium* Gingins §§ *Mexicanae* Becker].

Herb, acaulescent, stoloniferous, the stolons slender, elongated, up to 20 cm long or more. *Leaves* with the petioles very slender, up to 10 cm long, glabrous, the stipules ± elliptic, acute, fimbrillate, up to 1 cm long, membranous, glabrous, greenish-white; blade subcircular or circular-reniform, deeply cordate at the base, short-pointed at the apex, crenulate-serrulate at the margins, up to 3.8 cm long and wide, membranous, sparsely appressed-hyaline-puberulous on both sides.

Flowers with the pedicels filiform, up to 14 cm long, the bracteoles triangular, acute, 5-6 mm long and 2.2-2.8 mm wide; sepals ovate, acute, 4.5-5.5 mm long and 1.8-2.2 mm wide, the basal auricles rounded and ca 1 mm long; anterior petal obovate, broadly rounded at the apex, 13 mm long (spur included) and 6 mm wide, the spur small, scarcely 2 mm long; lateral and upper petals oblong-obovate, unguiculate, rounded at the apex, 11.5-13 mm long and 4.5-5 mm wide; anthers ca 1.8-2 mm long, the connective appendages very broadly oblong-ovate, irregularly truncate at the apex, ca 1.5 mm long and wide; ovary ellipsoid, ca 2 mm long; style ca 2 mm long, slightly geniculate above the base, clavate towards the apex, the apex depressed-capitate, marginate and with a small beak abaxially. *Capsule* ellipsoid, ca 6-6.5 mm long.

From southern Mexico to Panama.

CHIRIQUÍ: wooded hillside nr El Potrero, Chiriquí Volcano, alt 2800 m, *Killip 3602* (US); Potrero Muleto to summit, Volcán Chiriquí, alt 3500-4000 m, *Woodson & Schery 406* (MO, US).

This species is very closely related to and perhaps even conspecific with *V. hookeriana* H. B. K. (Nov. Gen. Sp. Pl. **5:** 369, *t. 492(2)*, 1821), *V. nannei* Polak. (Linnaea **41**: 547, 1877), and *V. seleriana* Becker (Repert. Sp. Nov. **20:** 6, 1924).

2. **Viola odorata** L., Sp. Pl. 934, 1753 [§ *Nomimium* Gingins §§ *Uncinatae* Kupffer].

Herb, acaulescent, stoloniferous. *Leaves* with the petioles up to 9 cm long, the stipules narrowly ovate, acuminate, up to 1.5 cm long, glandular-fimbrillate; blade subcircular, deeply cordate at the base, obtuse at the apex, crenulate at the margins, up to 5.2 cm long and wide, membranous, with scattered, appressed, hyaline, short hairs on both surfaces and along the margins. *Flowers* with the pedicels up to 9 cm long, the bracteoles narrowly triangular, acute, ca 6 mm long and 1.5 mm wide at the base, minutely glandular-fimbrillate; sepals ovate, acute, ca 10 mm long (basal auricles included) and 3-4 mm wide, the basal auricles ca 3 mm long and fimbrillate at the base; corolla purple; anterior petal oblong-obovate, rounded at the apex, 15 mm long (spur included) and 6 mm wide, the spur ca 4 mm long; lateral and upper petals oblong-obovate to obovate, rounded at the apex, 12 mm long and 5-7 mm wide; anthers ca 2 mm long, the connective appendages deltoid, ca 1.5 mm long and wide at the base; ovary ovoid, as long as the anthers; style ± geniculate at the base, enlarged towards the apex, ca 2.5 mm long, the apex unciform. *Capsule* ellipsoid, ca 7-8 mm long, puberulous.

Native to Europe, North Africa, and Asia; introduced.

CHIRIQUÍ: Alto Lino, alt 4200 ft, wayside flower, very well naturalized, *Bro. Maurice 854* (US).

3. **Viola stipularis** Sw., Nov. Gen. Sp. Pl. Prodr. 117, 1788; Fl. Ind. Occ. 1956, 1806 [§ *Leptidium* Gingins emend. Becker].—Fig. 3.

Herb, glabrous, the rhizomes creeping, lignous, often elongated, the stems ± erect, up to 20 cm long. *Leaves* with the petioles up to 8 mm long, the stipules narrowly triangular, up to 2 cm long, long-fimbrillate, brownish; blade oblique, narrowly elliptic, cuneate at the base, long-acuminate at the apex, crenulate-serrulate at the margins, up to 9.5 cm long and 3.2 cm wide. *Flowers* with the pedicels filiform, up to 6 cm long, the bracteoles subulate, 5-7 mm long; sepals narrowly ovate, acute, ca 6 mm long and 1.2 mm wide; corolla white with purple veins; anterior petal obovate, rounded at the apex, ca 9 mm long (spur included) and 4.5 mm wide, the spur only ca 1 mm long; lateral and upper petals oblong-ovate or oblong-elliptic, rounded at the apex, ca 6.5-7.5 mm long and 2-3 mm wide; anthers ca 1.8 mm long, the connective appendages deltoid, ca 1 mm long and wide at the base, brownish, inconspicuously fimbrillate; ovary ca as long as the anthers; style slender, terete, ± erect, ca 2.8 mm long, with the indistinct stigma aperture at the apex. *Capsule* oblong-ellipsoid, ca 6-7 mm long, the seeds ca 1 mm long.

Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, and the Lesser Antilles.

COCLÉ: hills N of El Valle, alt 850 m, *Allen 2978* (MO).

4. **Viola scandens** Schult. in Roem. & Schult. in L., Syst. Veg. ed. nov., **5:** 391, 1819 [§ *Leptidium* Gingins emend. Becker].

Herb with the stems creeping or climbing, much-branched, up to 30 cm long or more, glabrous. *Leaves* with the petioles up to 8 mm long (in the only Panamanian collection, but up to 25 mm long in extra-Panamanian collections), the stipules narrowly oblong-ovate, acute, fimbrillate, up to 5 mm long and 1 mm wide; blade triangular-ovate, cordate and with broad sinuses at the base, acute at the apex, crenulate-serrulate and often with cartilaginous teeth at the margins, up to 18 mm long and 15 mm wide (usually larger in extra-Panamanian collections). *Flowers* with the pedicels filiform, longer than the leaves, up to 25 mm long, the bracteoles subulate, ca 3 mm long; sepals narrowly ovate, acuminate, ca 4.5-5 mm long and 1.2 mm wide, the basal auricles short and rounded; corolla white with purple veins; anterior petal ± oblong, truncate and mucronulate at the apex, ca 8.5 mm long (spur included) and 4 mm wide, very shortly calcarate; lateral and upper petals obovate, ± rounded at the apex, ca 7-7.5 mm long and 2.5-3 mm wide; anthers ca 1.5 mm long, the connective appendages deltoid, acute or acuminate, ca 1.5-1.8 mm long and 1 mm wide at the base; ovary oblong-ellipsoid, ca 1.5 mm long; style erect, terete, gradually tapering towards the apex, ca 2.5 mm long, the apex beakless. *Capsule* oblong-ellipsoid, ca 5 mm long, topped by the persistent style.

Mexico, Central America, Venezuela, Colombia, Ecuador, and Bolivia.

CHIRIQUÍ: valley of upper Río Chiriquí Viejo, Cerro Pando, *White 9* (MO).

Fig. 3. *Viola stipularis* Sw.: A, habit (×½); B, flower (×4); C, anterior petal (×4); D, lateral petal (×4); E, upper petal (×4); F, anther (×10); G, gynoecium (×7); H, capsule (×4); I, seed (×10). A-G after *Allen 2978* (MO); H-I after *Skutch 3192* (MO), Costa Rica.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 129. TURNERACEAE[1]

BY ANDRÉ ROBYNS[2, 3]

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St. Louis, Missouri

Herbs, annual or perennial, or shrubs, infrequently trees, glabrous to often pubescent, the hairs simple or sometimes stellate. *Leaves* alternate, simple, usually petiolate, sometimes sessile, the stipules small or absent, the blade entire to lobed, often 2-glandular basally. *Flowers* mostly axillary and solitary, rarely in racemes, panicles or cymes, hermaphrodite, actinomorphic, homo- or heterostylous; pedicels free or adnate to the petioles of the subtending leaves, usually 2-bracteolate; hypanthium usually present, sometimes very short or wanting, deciduous, often with 5 protuberances above the insertion of the stamens; sepals 5, imbricate; petals 5, usually inserted in the hypanthium, often unguiculate; corona of glandular scales often present within the petals at the apex of the claw; stamens 5, usually inserted in the hypanthium, the filaments free, often flattened or narrowly alate, the anthers introrse, dorsifixed, 2-thecate, longitudinally dehiscent; pollen grains usually 3-colporate, reticulate; gynoecium of 3 syncarpous carpels; ovary superior (to sometimes subinferior), 1-locular, with 3 parietal placentae, the ovules usually ∞, anatropous, rarely with 1 basal ovule; styles 3, terminal, slender, the stigmas usually penicellate or laciniate. *Fruits* capsular, loculicidally or septicidally 3-valvate; seeds curved or not, unilaterally arillate, the testa crustaceous, often alveolate-striate; endosperm copious and carnose; embryo straight or slightly arcuate; cotyledons plano-convex, foliaceous.

A tropical and subtropical family of eight genera in America and Africa, but particularly well represented in tropical America; three genera reported from Panama.

According to Rao (Jour. Ind. Bot. Soc. **28:** 198-201, 1949), the hypanthium is not of receptacular origin, but appendicular in nature and the perigyny (in

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[1] Assisted by National Science Foundation Grant No. GB-170 (Principal Investigator, H. C. Cutler).

[2] Visiting Curator of the Flora of Panama, Missouri Botanical Garden; *Chargé de Recherche* of the National Foundation for Scientific Research, Belgium.

[3] I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and for the loan of material: Field Museum of Natural History, Chicago, Illinois (F) and U. S. National Herbarium, Washington, D. C. (US).

Turnera) results from the adnation of the basal parts of calyx, corolla and androecium.

Useful references:

Brizicky, G. K., The genera of *Turneraceae* and *Passifloraceae* in the southeastern United States. Jour. Arnold Arb. **42:** 204-218, 1961.

Gilg, E., *Turneraceae* in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, **21:** 459-466, 1925.

Urban, I., Monographie der Familie der Turneraceen. Jahrb. K. Bot. Gart. Mus. Berlin **2:** 1-152, *t. 1-2,* 1883.

a. Trees 7-30(40) m tall; hypanthium wanting ..... 1. *Erblichia*
aa. Herbs or shrubs; hypanthium distinct.
  b. Corona present; styles dichotomously divided nearly to the base ..... 2. *Piriqueta*
  bb. Corona absent; styles simple ..... 3. *Turnera*

1. ERBLICHIA

Erblichia Seem., Bot. Voy. Herald *t.* 27, 1853, 130, 1854.

Piriqueta Aubl. sect. *Erblichia* (Seem.) Urban, Jahrb. K. Bot. Gart. Mus. Berlin **2:** 78, 1883.

Shrubs or small to tall trees, the hairs simple. *Leaves* grouped towards the apex of the branchlets, the stipules minute, the blade eglandular basally. *Flowers* large (at least in tropical North America), axillary, solitary, homostylous, the prophylls foliaceous, the pedicels free, articulate below the middle; receptacle subcupular-shaped; sepals borne on the receptacle, caducous; petals obovate, short-unguiculate, yellow, orange or red, caducous; corona of fimbrillate glandular scales present; filaments dilated towards the base, the anthers linear-oblong, straight or curved; ovary oblong-ellipsoid, glabrous to pubescent, with 3 ∞-ovulate placentae; stigmas dilated, fimbrillate. *Capsules* loculicidal to the middle, the pericarp muricate, glabrous to pubescent; seeds with the testa smooth to longitudinally striate.

A genus of five species distributed in Madagascar (3 sp.), South Africa (1 sp.), and southern Mexico and Central America (1 sp.).

According to van Steenis-Kruseman & Stearn (in *Dates of Publication* in Fl. Males., Ser. 1, **4:** CCXII, 1954), plate 27 (in Seem., Bot. Voy. Herald) was published in 1853, while the description of *E. odorata* Seem. appeared only in 1854. The date of publication of the genus *Erblichia* is therefore 1853 instead of 1854.

Erblichia was reduced to synonymy under *Piriqueta* by Urban (loc. cit.) and treated as such by Gilg in Engler & Prantl, Nat. Pflanzenfam. ed. 2, **21:** 464, 1925, and by Perrier de la Bâthie in Humbert, Fl. Madagascar, Fam. 142 Turnéracées 7-12, 1950. With Standley & Williams (in *Flora of Guatemala,* Fieldiana: Bot. **24**(7): 110-112, *fig. 13,* 1961) I consider *Erblichia* as a genus readily separated from *Piriqueta* by the minutely stipulate leaves and by the sepals borne on the receptacle instead of on a distinct hypanthium (cf. also Hutchinson, The Families of Flowering Plants **1:** 237, 1959).

1. **Erblichia odorata** Seem., Bot. Voy. Herald *t.* 27, 1853, 130, 1854.

Piriqueta odorata (Seem.) Urb., Jahrb. K. Bot. Gart. Mus. Berlin **2:** 80, 1883.
P. xylocarpa Sprague & Riley, Kew Bull. **1923:** 373, 1923.
Erblichia xylocarpa (Sprague & Riley) Standley & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 353, 1940.
E. standleyi Steyerm., loc. cit. 356, 1940.

Tree 7-30(40) m tall, the trunk up to 1 m in diam at the base, the branchlets glabrous (in the only Panamanian collection seen) to velutinous. *Leaves* with the petiole canaliculate above, up to 1 cm long, the stipules to 1 mm long, puberulous; blade narrowly elliptic to narrowly oblong-elliptic, acute and decurrent at the base, acute to long-acuminate at the apex, crenate to remotely crenulate-serrulate at the margins, to 14 cm long and 4 cm wide, chartaceous, lustrous and glabrous above, slightly paler, glabrous or nearly so, and with the costa prominent beneath. *Flowers* with the peduncles to 4.5 cm long, to 7.5 cm long in fruit, glabrous or nearly so, the prophylls subopposite, the pedicels to 2.5-3 cm long, glabrous to sparsely appressed-puberulous; sepals narrowly ovate to linear-ovate, long-acuminate, to 6 cm long, green or yellowish-green, some with yellow (or pale orange or salmon) margins, sparsely appressed-puberulous to glabrous outside; petals cuspidate to caudate at the apex, to 8 cm long and 4.5 cm wide, yellow (or reddish-orange); filaments to 4.5 cm long, glabrous or densely villosulous below, the anthers straight, to 6 mm long, appendiculate at the apex; ovary glabrous to densely velutinous; styles to 5 cm long, glabrous or sparely appressed-puberulous below. *Capsules* (according to Sprague & Riley, loc. cit.) ellipsoid, ligneous, to 3.3 cm long and 1.7 cm wide, glabrous; seeds obovoid, slightly curved, to 4.5 mm long, longitudinally striate.

Southern Mexico and Central America.

E. odorata is extremely variable especially in indumentum and color of calyx and corolla.

CHIRIQUÍ: Paredes I, on outskirts of woods, *Seemann s.n.* (type K, not seen). COCLÉ: El Valle de Antón, trail to Las Minas, alt 1000 m, scattered throughout forest, *Allen 2468* (F, MO, US).

2. PIRIQUETA

Piriqueta Aubl., Hist. Pl. Gui. Fr. 298, 1775.

Herbs, annual or perennial, or small shrubs, the indumentum of simple and stellate hairs. *Leaves* sessile or petiolate, estipulate, the blade with the margins crenate or serrate, rarely entire, usually eglandular basally. *Flowers* axillary, usually solitary, sometimes in cymose inflorescences, homo- or heterostylous, the pedicels free, the bracteoles absent or minute; hypanthium present; petals inserted at the apex of the hypanthium, cuneate or slightly unguiculate at the base, yellow or orange; corona membranous, fimbrillate, inconspicuous; stamens inserted towards the base of the hypanthium, the anthers with the apex often recurved after anthesis; ovary with 3 ∞-ovulate placentae; styles 3, dichotomously divided nearly to the base; stigmas penicillate. *Capsules* loculicidal almost to the base, the pericarp

smooth or tuberculate; seeds numerous, straight or curved, foveolate-striate to alveolate.

A New World genus of about 25 species, mainly tropical but with one extension into the warmer temperate zone of eastern North America; one species at present reported in Panama and Central America.

1. **Piriqueta cistoides** (L.) Meyer ex Steud., Nom. Bot. ed. 2, **2:** 344, 1841.—Fig. 1.

Turnera cistoides L., Sp. Pl. ed. 2, 387, 1762.

Herb, annual, the stems erect, simple or branched, puberulous and hirsute-hispid with long, spreading, brownish hairs, these simple and/or stellate. *Leaves* very variable, the petiole to 8 mm long, the upper leaves sometimes almost sessile; blade elliptic, narrowly elliptic or narrowly ovate, sometimes lanceolate-linear to linear, acute to sometimes rounded at the base, acute or obtuse at the apex, serrate to crenate-serrate at the margins, sometimes entire-margined or almost so, to 4 cm long and 1.4 cm wide, usually densely stellate-pubescent on both sides, the hairs many-rayed and with one of the rays often elongated and stiff. *Flowers* solitary, homostylous, the pedicels slender, to 1.5 cm long, elongated in fruit, with the same indumentum as the stem, ebracteolate; hypanthium ca 2 mm long; sepals narrowly triangular, ca 4 mm long, usually densely stellate-puberulous; petals obovate, cuneate at the base, ca 8 mm long, yellow or orange; corona less than 0.5 mm long; filaments ca 3.25 mm long, glabrous; anthers ca 1.25 mm long, the apex recurved at anthesis; ovary ovoid, ca 2 mm long and 1.25 mm wide, densely appressed-hirsute; styles ca 2.25 mm long, glabrous. *Capsules* ovoid to globose, to 7 mm long, the valves smooth, appressed-hirsute and with simple hairs; seeds almost straight, oblong-obovoid, ca 1.5-2 mm long, the testa foveolate-striate to alveolate.

Southern Mexico, Central America, West Indies, and South America.

COCLÉ: vic of Nata, alt 50 m, *Allen 836* (F, MO, US). PANAMA: Tumba Muerto Rd, nr Panama City, grassy field, *Standley 29768* (US); Taboga I, along high trails, up to 300 m alt, *Allen 108* (MO); id., grassy upland slopes, *Macbride 2820* (F, US); id., alt ca 0-186 m, *Woodson et al. 1465* (F, MO).

3. TURNERA

Turnera L., Sp. Pl. 271, 1753; Gen. Pl. ed. 5, 131, 1754.

Herbs, annual or perennial, suffrutices, shrubs, or infrequently trees, the hairs usually simple, rarely stellate. *Leaves* petiolate, the stipules minute or absent, the blade entire-margined or the margins variously toothed, often 2-glandular at the base. *Flowers* usually solitary in the axils of the uppermost leaves, rarely in cymose or capitate inflorescences, homo- or heterostylous; pedicels free or ± adnate to the petioles of the subtending leaves; bracteoles sometimes foliaceous; hypanthium present; petals inserted at or near the apex of the hypanthium, obovate, cuneate or unguiculate at the base, variously colored, but often yellow; corona

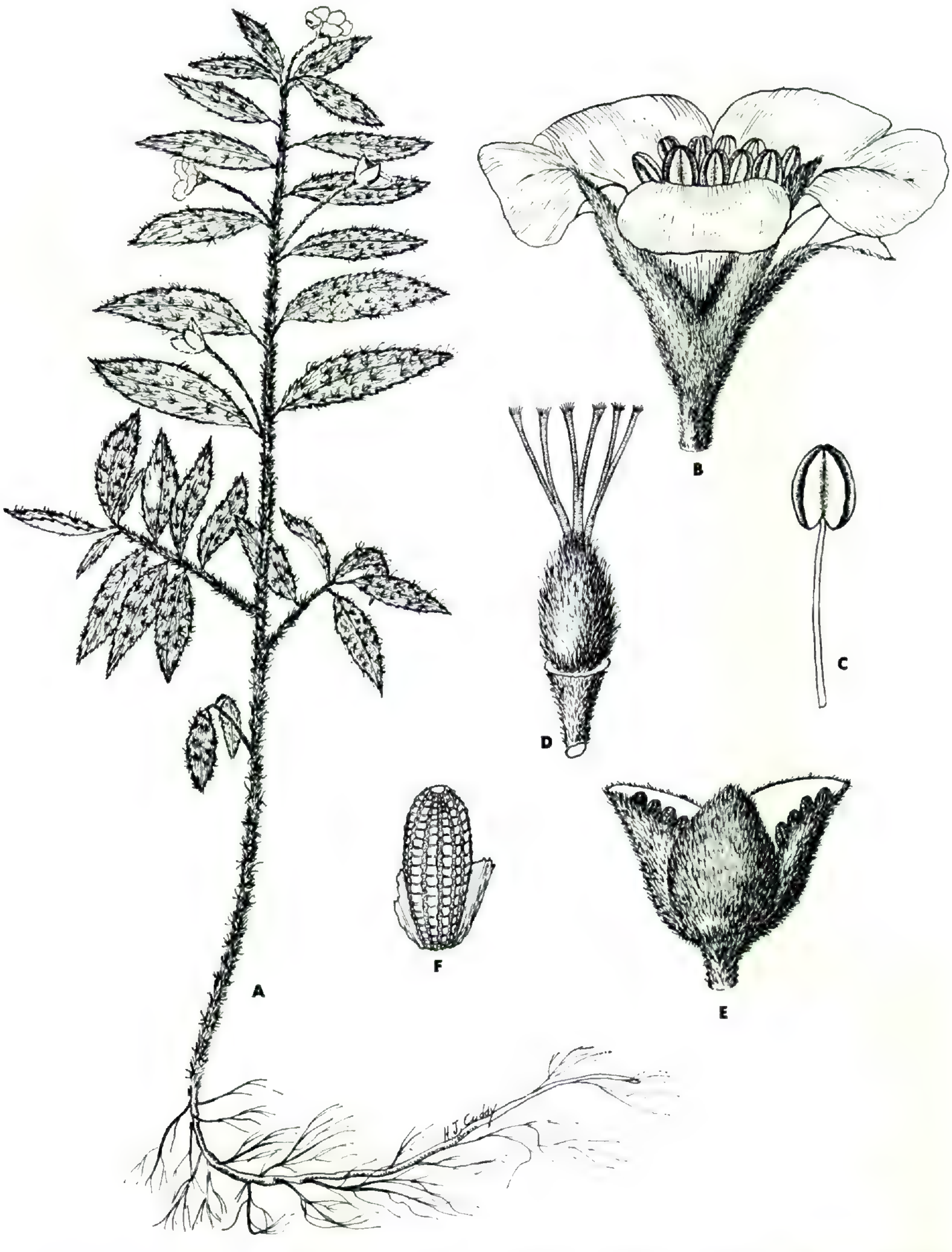

Fig. 1. *Piriqueta cistoides* (L.) Meyer ex Steud.: A, habit (×½); B, flower (×5); C, stamen (×8); D, gynoecium (×8); E, dehiscent capsule (×3); F, arillate seed (×10). After *Allen 108* (MO).

wanting; stamens inserted near the base, ± in the middle, or near the apex of the hypanthium, the lower parts of the filaments broadened and adnate by their membranous margins to the hypanthium forming 5 nectariferous pockets; ovary with 3 ∞-ovulate placentae; styles simple; stigmas penicillate or flabellate. *Capsules* loculicidal to below the middle or almost to the base, the pericarp rather thick, smooth to tuberculate; seeds straight or curved, the testa striate-foveolate.

A New World genus of about 60 species, ranging from Texas to Argentina, but primarily tropical; some species introduced in the Old World tropics; three species at present reported from Panama.

a. Leaf-blades eglandular at the base; pedicels free; capsule glabrous; seeds rather densely whitish-puberulous ..... 1. *T. panamensis*

aa. Leaf-blades usually conspicuously 2-glandular at the base; pedicels adnate to the petioles of the subtending leaves; capsule with indumentum; seeds glabrous.

b. Bracteoles foliaceous ovate, the lower half deeply incised, the apex long-acuminate, 15-30 mm long ..... 2. *T. angustifolia*

bb. Bracteoles linear-subulate, to 10 mm long ..... 3. *T. ulmifolia*

1. **Turnera panamensis** Urb., Jahrb. K. Bot. Gart. Mus. Berlin **2:** 92, 1883.—Fig. 2.

T. salicifolia Seem., Bot. Voy. Herald 130, 1854, non Camb. (in St.-Hil. *et al.*, Fl. Bras. Merid. **2:** 229, 1830).

T. hindsiana Hemsl., Biol. Centr.-Amer. **1:** 474, 1880, non Benth. (Bot. Voy. Sulphur 101, 1844).

Shrub 0.5-4.0 m tall, the branchlets puberulous. *Leaves* with the petioles canaliculate above, to 5 mm long, puberulous, the stipules subulate, to 4 mm long; blade ovate, elliptic, narrowly elliptic or narrowly ovate-elliptic, the base acute and decurrent, the apex bluntly acuminate, the margins crenate, the crenae at first glandular, later usually submarginate, to 18 cm long and 6 cm wide, chartaceous, subglabrous above, puberulous beneath, becoming glabrescent, the costa and secondary veins prominent beneath. *Flowers* axillary and solitary, often approximate on abbreviated branchlets, heterostylous; peduncles to 6 mm long, puberulous, the bracteoles stipule-like, to 5.5 mm long, inconspicuously 2-stipulate; pedicels to 7 mm long, puberulous; hypanthium 4-5 mm long, puberulous; sepals narrowly triangular, long-acuminate-aristate, 12-15 mm long, puberulous outside, 3-veined; petals inserted near the throat of the hypanthium, long-unguiculate, 18-30 mm long, yellow, orange-yellow or orange; stamens inserted towards the base of the hypanthium, the filaments in short-styled flowers 10-12 mm long, in long-styled flowers to 6 mm long, glabrous, the anthers to 2 mm long; ovary oblong-ellipsoid, ca 3 mm long, glabrous to ± densely puberulous towards the apex; styles in short-styled flowers ca 5 mm long, in long-styled flowers to 8 mm long, glabrous to ± densely puberulous below; stigmas penicillate. *Capsules* subglobose-ellipsoid, 6-8 mm long, dark brown, the pericarp densely tuberculate, glabrous; seeds narrowly pyriform, slightly curved to almost straight, 4-5 mm long, rather densely whitish-puberulous.

Fig. 2. *Turnera panamensis* Urb.: A, habit (×½); B, long-styled flower, longitudinal section (ca ×2); C, short-styled flower, longitudinal section (ca ×2). A-B after *A. Robyns 65-20* (MO); C after *Dwyer 2411* (MO).

Known only from Panama.

CANAL ZONE: Barro Colorado I, *Aviles 109* (F), *Bailey & Bailey 340* (F), *Bangham 381* (F), *Kenoyer 452* (US), *A. Robyns 65-20* (MO), *Standley 41057* (US), *Wetmore & Abbe 103* (F), *103A* (F), *Wilson 25* (F), *Woodworth & Vestal 526* (F); Río Agua Salud, nr Frijoles, *Piper 5872* (US); vic of Gamboa, *Allen 1967* (MO), *Pittier 6639* (US); in Gamboa Distr, along jungle trail, *Maggs II 42* (F); vic of Summit, alt 500 ft, in heavy forest & margins, *Allen 4517* (F, MO, US); Cerro Gordo, nr Culebra, wet thicket, *Standley 25963* (US); Río Pedro Miguel, nr East Paraíso, moist forest, *Standley 29959* (US); Cocoli, *Seemann 549* (syntype, photo MO); Albrook, U. S. Army Tropic Test Center Site, *Dwyer & A. Robyns 113* (MO); Rd C-21, *Duke 5775* (MO). PANAMA: Sabanas, *Bro. Paul 322* (US); Juan Díaz, rocky stream bed, *Killip 3416* (US); Tocumen Airport, *Dwyer 2411* (MO); Río Tocumen, moist thicket, *Standley 29473* (US); banks of lower Río Cabra, *Bro. Maurice 795* (US); banks of Mamoni River, above Chepo, alt 20-25 m, *Pittier 4728* (US). PROVINCE UNKNOWN: *Hayes 114* (syntype, not seen).

2. **Turnera angustifolia** Mill., Gard. Dict. ed. 8, 1768.

T. ulmifolia L. var. *angustifolia* (Mill.) Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **1:** 1503, 1798; Urb., Jahrb. K. Bot. Gart. Mus. Berlin **2:** 141, 1883.

Shrubs (or herbs?) 0.3-1.8 m high, the branchlets sparsely appressed-puberulous when young. *Leaves* with the petiole slender to rather thick, canaliculate and often with a grayish gland near the apex above, 6-22 mm long, sparsely puberulous; blade ovate to narrowly ovate, cuneate, decurrent and conspicuously 2-glandular at the base, acute to acuminate at the apex, coarsely crenate or serrate at the margins, 5-13.5 cm long and 1.5-5.5 cm wide, thin-chartaceous, slightly discolor, the costa and secondary veins prominent beneath, sparsely puberulous especially along the veins on the lower surface. *Flowers* solitary in the axils of the uppermost leaves, homostylous, the pedicels as long as or slightly longer than the petioles of the subtending leaves and adnate to them, the bracteoles foliaceous, sessile, ovate, the lower half deeply incised, the apex long-acuminate, 15-30 mm long, sparsely puberulous; hypanthium ca 10 mm long, sparsely puberulous; sepals narrowly triangular, acuminate-aristate, 12-15 mm long, sparsely puberulous outside; petals inserted near the apex of the hypanthium, unguiculate, 30-40 mm long, yellow; stamens inserted in the middle of the hypanthium, the filaments ca 14 mm long, glabrous, the anthers narrowly sagittate, ca 5 mm long; ovary ovoid-conical, ca 2 mm long and wide at the base, minutely sericeous, the styles ca 16 mm long, the stigmas penicillate. *Capsules* globose, 7-10 mm in diam, the pericarp greenish, muricate and puberulous; seeds oblong, slightly curved to almost straight, ca 2.5 mm long and 1 mm wide, glabrous.

Along the Atlantic coast from Nicaragua to Panama, and the West Indies; introduced in the East Indies and Madagascar.

According to Brizicky (Jour. Arnold Arb. **42:** 208, 1961), *T. angustifolia* (as West Indian *T. ulmifolia* L. var. *ulmifolia* = var. *angustifolia*) "has been recorded as naturalized . . . on the Florida Keys and in peninsular Florida."

BOCAS DEL TORO: Bocas del Toro I Airport, *Lewis et al. 778* (MO); vic of Chiriquí Lagoon, *von Wedel 1307* (MO, US), *1352* (MO); id., Water Valley, *von Wedel 1739* (MO, US); id., Johns Creek, *von Wedel 2767* (MO, US); id., Isla Colón, *von Wedel 53* (MO), *104* (MO), *513* (MO), *2940* (MO); id., Old Bank I, *von Wedel 1954* (MO, US), *2103* (MO, US).

This species is generally considered a variety of *T. ulmifolia.* The difference between the bracteoles of both taxa, however, is so striking that I consider *T. angustifolia* to be a distinct species. All the collections of this species which I have seen from Panama, Costa Rica, and Nicaragua were erroneously determined as *T. panamensis.*

Turnera angustifolia is beautifully illustrated in Curtis's Botanical Magazine **8:** *t. 281,* 1794.

3. **Turnera ulmifolia** L., Sp. Pl. 271, 1753.

Herb, erect, or small shrub, the branchlets usually densely pilose throughout, the hairs simple, pale, often appressed upwards. *Leaves* short- to moderately long-petiolate, the petiole to 10 mm long, usually densely appressed-puberulous; blade elliptic to narrowly elliptic, sometimes almost linear, infrequently obovate, the base attenuate-cuneate and conspicuously 2-glandular, sometimes inconspicuously so or rarely eglandular, the apex acute to rarely subacute, the margins serrate-crenate especially above the half, to 5 cm long and 2 cm wide, thin-chartaceous, puberulous on both sides, but the indumentum always denser and often grayish beneath, the costa and secondary veins slightly prominent below. *Flowers* axillary, solitary, heterostylous; pedicels shorter than to equalling the petioles of the subtending leaves and adnate to them; bracteoles linear-subulate, to 10 mm long and ca 0.5 mm wide, puberulous; hypanthium ca 5-7 mm long, puberulous; sepals narrowly triangular, ca 9-11 mm long and 2 mm wide at the base, puberulous outside; petals inserted near the throat of the hypanthium, long-unguiculate, to 22 mm long, yellow, sometimes dark purple or brownish at the base; stamens inserted towards the base of the hypanthium, the filaments in short-styled flowers to 12 mm long, in long-styled ones to 8 mm long, the anthers ca 3 mm long; ovary densely sericeous; style in short-styled flowers ca 5 mm long, in long-styled ones to 10 mm long, the stigmas densely penicillate. *Capsules* broadly ellipsoid, ca 3-4 mm high, the pericarp greenish, tuberculate and densely sericeous to sparsely short-pilose; seeds slightly arcuate, ca 2.5 mm long, glabrous.

A species highly variable vegetatively and distributed throughout the range of the genus.

CHIRIQUÍ: Francés Arriba School, ca 14 mi N of David, alt 1200 ft, *Lewis et al.* 652 (MO); 5 mi S of Boquete toward David, elev 2800 ft, common along rd, *McDaniel* 6795 (MO); llanos W of Gualaca, alt 500 ft, *Allen* 5043 (MO). COCLÉ: vic of Olá, alt 100-350 m, *Pittier* 5057 (US); Aguadulce, in savannas nr sea level, *Pittier* 4878 (US); Penonomé, *Ebinger* 1009 (MO), *Williams* 183 (US); betw Las Margaritas & El Valle, *Woodson et al.* 1717 (MO); Antón, *Dwyer* 7040 (MO); Río Hato Airstrip, *Blum & Dwyer* 2476 (MO), *Burch et al.* 1128 (MO); Santa Clara beach, *Ebinger* 1137 (MO), *Woodson et al.* 1699 (F, MO), 1701 (F, MO); La Venta, *Allen* 2967 (MO). LOS SANTOS: Pocri, *Dwyer* 1121 (MO); Playa de la Concepción, *Burch et al.* 1262 (MO). PANAMA: Río Mar, *Dwyer* 1801 (MO), *Ebinger* 495 (MO), *Tyson et al.* 2314 (MO); San Carlos, *Dwyer* 4259 (MO); Sabanas N of Panama City, *Bro. Paul* 426 (US); along rd betw Panama City & Chepo, *Dodge et al.* 16682 (MO); along rd to Río Pacora, alt ca 50 m, *Allen* 818 (F, MO, US). VERAGUAS: ca 5 mi NE of La Mesa, *Blum & Tyson* 655 (MO).

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ERRATA

Page 46, legend of Fig. 2. For 'B, bract (×½); C, sepal (×½); D, petal (×½); E, androecium and gynoecium (×1)' read 'C, bract (×½); D, sepal (×½); E, petal (×½); B, androecium and gynoecium (×1)'

Page 74, line 30. For 'the scales are about as long as the anthers' read 'the scales are about ½ as long as the anthers'

Page 179, line 17. For '*Commelina virginica* L.' read '*Commelina erecta* L.'

Page 187, line 9. For '*Odum 2273*' read '*Blum, Duke & Odum 2273*'

Page 200, lines 22 & 23. For '(as observed in Johnston 3426, DAV), although seeds of Panama plant differences.' read 'fruits of *B. macrophylla* are collected, these may prove to show additional differences.'

Page 363, line 18. For 'flower' read 'flowers'

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THE BIOTIC RELATIONSHIP OF ANTHOCEROS AND PHAEOCEROS TO CERTAIN CYANOPHYTA[1]

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ABSTRACT

When the *Nostoc* isolates entered into thalloid cavities of *Anthoceros* and *Phaeoceros* and produced the typical globose endophytic colonies and/or when the algal isolate grew upon the nitrogen-free substrate in intimate contact with the thalli, chlorosis in the experimental cultures was not present to the degree that it occurred in the control cultures. These observations suggest the ability of these blue-green algal isolates to fix atmospheric nitrogen and to provide an available source to the liverworts used in these experiments. Cytochemical and ultrastructural observations further suggest that the algal endophyte may also benefit from this relationship if the algae are able to catabolize carbohydrate components of the mucilaginous thalloid cavity.

The presence of blue-green algae in thalli of *Anthoceros* was first reported by Hofmeister (1862) who thought the dark, blue-green, roundish masses in the thallus to be gemmae. However, careful investigations by Leitgeb (1881) showed that they were *Nostoc* colonies within the mucilaginous *Anthoceros* cavities. He reported that the endophytism is effected by the movement of free *Nostoc* hormogonia through slit-like openings into the mucilage cavities. Once within the cavities the hormogonia grow into globular colonies. The presence of *Nostoc* within the thallus causes an increased, attenuated growth of the cells surrounding the cavity. According to Campbell (1918) and Parihar (1961) the "host" cells produce tubular filaments which ramify through the algal mass and become so interwoven with it that sections appear as loose parenchyma with *Nostoc* filaments occupying the interstices. The writer can confirm their observations.

Pierce (1906) reported that the presence of the endophytic blue-green alga was not necessary for growth of the gametophyte, and that in fact thalli grown

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[1]Rewritten portion of a thesis submitted in partial fulfillment for the Doctor of Philosophy degree at the University of Texas.

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on sterilized soil without *Nostoc* grew better than those containing the alga. He further commented that there was no conceivable advantage in the enlargement of the mucilage chamber cells.

Since that time several investigators have isolated *Nostoc* from other sources—root parenchyma of *Gunnera* (Winter, 1934), roots of cycads, thalli of lichens, and the liverwort *Blasia* (Bond & Scott, 1955; Watanabe & Kiyohara, 1963)—and have been able to show through the use of isotopic nitrogen (N^{15}) the ability of the isolated algae to fix free nitrogen. None, however, has shown nitrogen fixation by a blue-green alga isolated from thalli of *Anthoceros*.

The purposes of this investigation were several: (1) to obtain axenic cultures of the blue-green algae isolated from thalli of *Anthoceros* spp. and *Phaeoceros* spp.; (2) to obtain and grow the thalli in axenic culture; (3) to attempt inoculation of the algal isolates into the thalli in culture utilizing a nitrogen-free medium; (4) to attempt inoculation of thalli with other blue-green algal isolates from other plants; and (5) to investigate the nature and specificity of the blue-green alga-liverwort relationship.

Materials and Methods

In June, 1961, collections of *Phaeoceros laevis* subsp. *carolinianus* (Michx.) Prosk. were made in Bastrop County, Texas. Additional specimens of this subspecies were collected in Jefferson County, Alabama, by T. E. Deason in the fall of 1962. Clonal, axenic cultures of these two collections were obtained by following the procedures of Näf (1958) as modified by Kelley & Postlethwait (1962). Two species of *Anthoceros* (H 13 *A. husnoti* Steph. and H. 166 *A. punctatus* L.) were obtained from the culture collection at the Czechoslavakian Academy of Sciences in Prague. These two living specimens were not axenic.

Of the blue-green algal isolates used in the experiment, seven strains were obtained from the blue-green algal collection maintained at the Czechoslavakian Academy of Sciences; two were supplied through the courtesy of Dr. Jack Meyers, and four were isolated from the collection of *Phaeoceros leavis* subsp. *carolinianus*, purified, and placed into axenic cultures in cooperation with Dr. Larry W. Jones. Collection and isolation data for all blue-green algal isolates used in the experiments are summarized in Table 1. The algal isolates were grown in 15 cm test tubes into which 10 ml of Bold's Basil Medium (BBM), lacking nitrogen, had been added (Bischoff & Bold, 1963). Transfers were made to new media every three weeks.

For the experiment sterile Petri dishes were divided into quadrants and partially filled with sterilized BBM nitrogen-deficient agar medium. Into the center of each quadrant a fragment (which contained at least one growing apex) of each of the four species of *Anthoceros* and *Phaeoceros* was transferred and carefully marked. To the surface of each of the four thalli per plate, three drops of a suspension of a given blue-green algal isolate were added. The preparations were then placed in an incubator in 250 ft c illumination at 15° with 12 hr diurnal light, and grown for 125 days.

Table 1. Collection data of the blue-green algal isolates.

Designation	Species	Isolator	Source
122*	*Anabaena variabilis*	Greifswald	unknown
123*	*Nostoc linckia*	unknown	unknown
373*	*Anabaena cylindrica*	Foog	unknown
388*	*Nostoc* sp.	Lhotský	*Blasia pusilla*
391*	*Nostoc* sp.	Lhotský	*Cycas circinalis*
393*	*Nostoc* sp.	Lhotský	*Encephalartos altensteinii*
395*	*Nostoc* sp.	Lhotský	*Gunnera chilensis*
396*	Nostoc sp.	Lhotský	*Stangeria paradoxa*
NMA	*Nostoc muscorum* A	unknown	unknown
NMB	*Nostoc muscorum* B	unknown	unknown
49	*Nostoc* sp.	Jones and Ridgway	*Phaeoceros laevis* (C. Texas)
50	*Nostoc* sp.	Jones and Ridgway	*Phaeoceros laevis* (W. Texas)
ND_1	*Nostoc* sp.	Jones	*Dion*
ND_2	*Nostoc* sp.	Jones	*Dion*

* Cultures obtained from the culture collection, Czechoslavakian Academy of Sciences, Prague.

Portions of thalli containing the endophytic alga were fixed for electron microscopy in 2% $KMnO_4$ and embedded in an Epon-Araldite mixture according to the methods of Mollenhauer (1959, 1964). Both thick (1μ) and thin sections of the specimens were cut on a Porter-Blum ultramicrotome. Thin sections were post-stained with 5% $Ba(MnO_4)_2$ to increase image contrast.

For light microscopy thalli containing endophytic algal colonies were fixed for 24 hr in formalin-acetic-acid, dehydrated, embedded in Tissuemat (mp 52.5°C), serially sectioned at 7μ, and placed on glass slides with Haupt's adhesive (Johansen, 1940; Jensen, 1962). Cytochemical procedures employed for localization studies were: the mercuric-bromphenol blue reaction (Mazia et al., 1953) for protein; the periodic acid-Schiff's reaction for insoluble carbohydrates (Hotchkiss, 1948); and ruthenium red to indicate the presence of pectic substances (Johansen, 1940).

RESULTS

The results of the experiments are summarized in Table 2. The control cultures were extremely chlorotic (Fig. 1) and only a few apices of the thalli remained green. In contrast, the experimental thalli were still green and growing vigorously (Fig. 2-4).

All but two of the *Nostoc* isolates entered into the thalli and produced typical endophytic colonies. No isolate of *Anabaena* formed endophytic colonies. However, usually both *Nostoc* and *Anabaena* isolates grew on the agar surface in intimate association with the thalli. In cases in which no entry of the algal isolate into the thalli was observed but in which a heavy growth of the alga occurred on the agar surface (Fig. 2), the thallus appeared almost normal. In cases in which the endophytic colonies developed within thalli (Fig. 3) without substantial growth of the alga on the surrounding agar surface, or cases in which both endophytic algal colonies were produced and substantial growth of the alga upon the substrate occurred (Fig. 4), little or no chlorosis of the thalli was observed. No hepatic species specificity was noted with respect to entry of the various *Nostoc* specificity was noted with respect to entry of the various *Nostoc* isolates used in

Table 2. Relation of *Nostoc* and *Anabaena* isolates and several *Anthoceros* and *Phaeoceros* species in culture.[a]

Algal strain	*P. laevis* (Tex.) E T A	*P. laevis* (Ala.) E T A	*A. husnoti* E T A	*A. punctatus* E T A
122	— P E	— P E	— P E	— P E
123	+ G E	+ G E	+ G E	+ G E
373[b]	— P Ec	— P Ec	— P E	— P E
388[b]	+ G E	+ G E	+ G E	+ G E
391[b]	+ G E	+ G E	+ P E	+ P E
393[b]	+ P E	+ P E	+ G E	+ G E
395[b]	+ G S	+ G S	+ G E	+ G E
396[b]	+ G E	+ G E	+ G E	+ G E
NMA	+ G S	+ G S	— P S	— P S
NMB	— P M	— P M	— P M	— P M
49	+ G E	+ G E	+ G E	+ G E
50	+ P S	+ P S	+ P S	+ P S
ND_1	— G Ec	— G Ec	— G Ec	— G Ec
ND_2	+ G S	+ G S	+ G E	+ G E
Control	— D —	— D —	— D —	— D —

[a] Readings were taken after 125 days. The letter designations on the above table are:
E = endophytic colonies formed (+ = present in the thalli, — = absent in the thalli.)
T = condition of the *Anthoceros* thallus (G = thallus green; P = thallus slightly chlorotic; D = only a few apices remaining alive.)
A = amount of blue-green algal growth upon agar surface (E = excellent; M = medium; S = slight; Ec = extremely heavy growth which covered portions of the thallus.)

[b] These algal isolates were obtained from endophytic colonies of other plants. See Table 1.

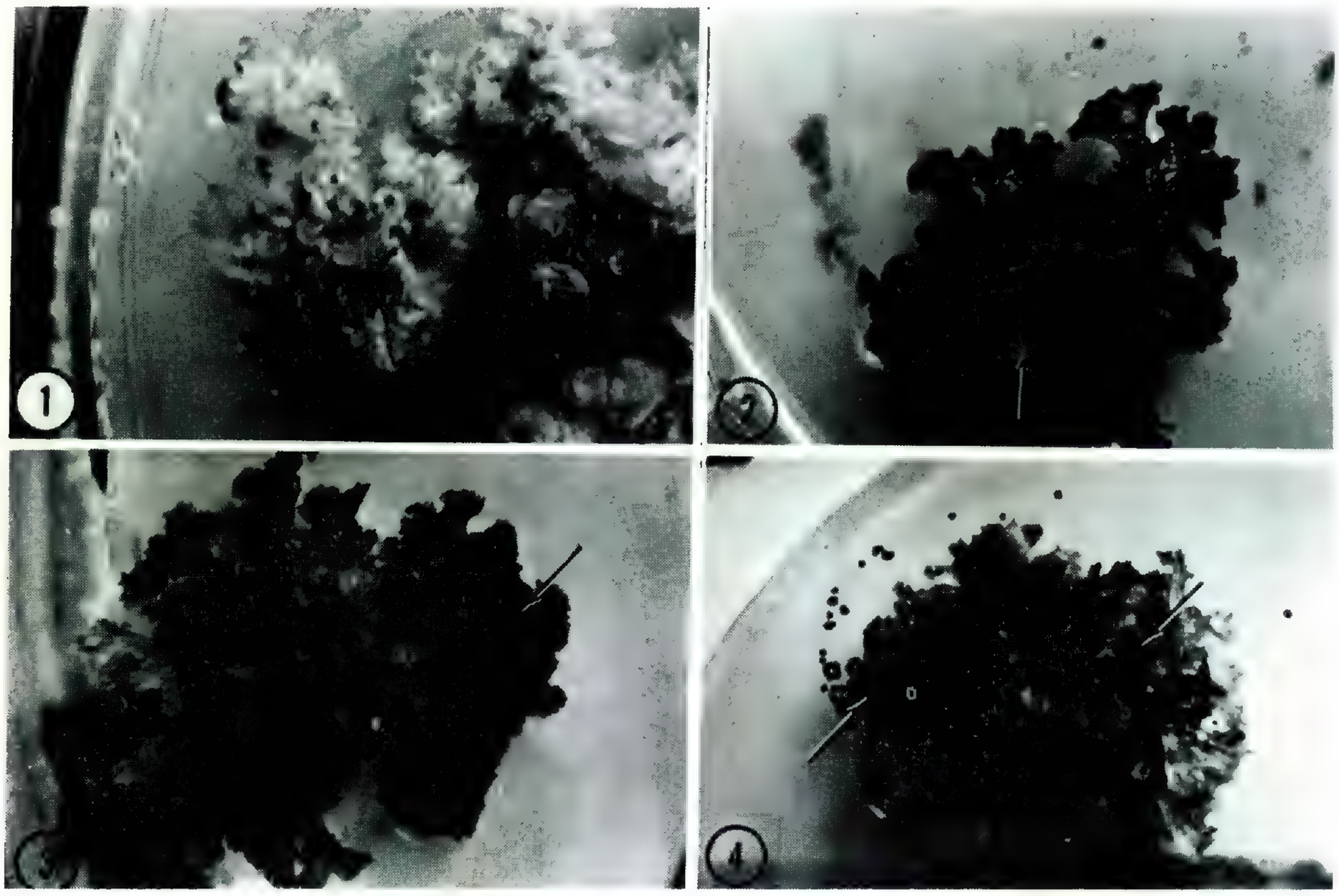


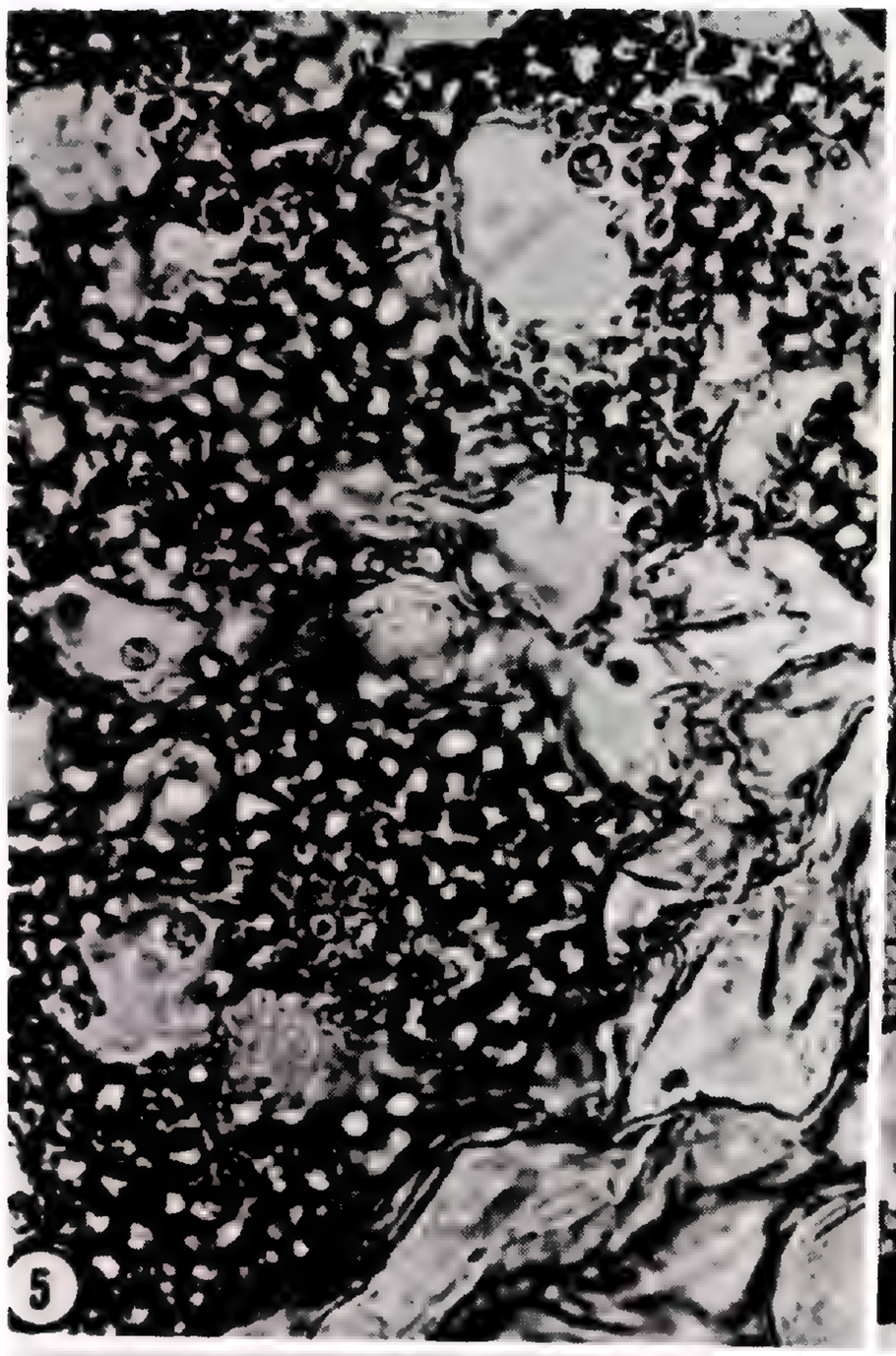
Fig. 1-4. Relation of *Anthoceros* to *Nostoc*. Fig. 1. *A. punctatus* 95 days after inoculation on nitrogen-deficient medium. Note the extremely chlorotic condition of the thallus, ×42. Fig. 2. *A. husnoti* which has been inoculated with *Nostoc* isolate ND_1. Note the absence of any endophytic colonies, but the presence of the heavy algal growth on the agar substrate (arrow), ×42. Fig. 3. *A. husnoti* which has been inoculated with *Nostoc* isolate NMA. Note the presence of endophytic algal colonies (arrow) but the absence of any algal substrate growth, ×42. Fig. 4. *A. husnoti* which has been inoculated with *Nostoc* isolate #49. Note the presence of endophytic algal colonies (arrow) and the presence of the algal growth upon the substrate, ×42.

this experiment—e.g. if a particular algal isolate formed endophytic colonies in one species of the hornwort, all other species were also endophytized.

In cytochemical investigations of the endophytic relationship, the mucilaginous matrix of the thalloid cavity in which the blue-green algae were embedded was PAS-positive, indicating the presence of carbohydrates. This mucilaginous substance also stained pink with ruthenium red, a classical dye indicator for the presence of pectic substances. In other sections which were stained by the mercuric bromphenol blue reaction, only the blue-green algae stained positively for the presence of protein; no staining reaction occurred within the mucilaginous matrix of the liverwort.

Light microscopic examinations of 1μ sections of the infected thalli revealed basic morphological differences between cells of the mucilaginous cavity wall and other cells of the thallus. Cells adjacent to the cavity or which projected into it (Fig. 5) contained smaller and less developed chloroplasts and fewer vacuoles.

Ultrastructural studies supported the above observations (Fig. 6, 7). In sections of the "host" cells adjacent to the cavity or in sections of these cells within the cavity there were fewer and smaller electron dense vacuoles present; subcellular



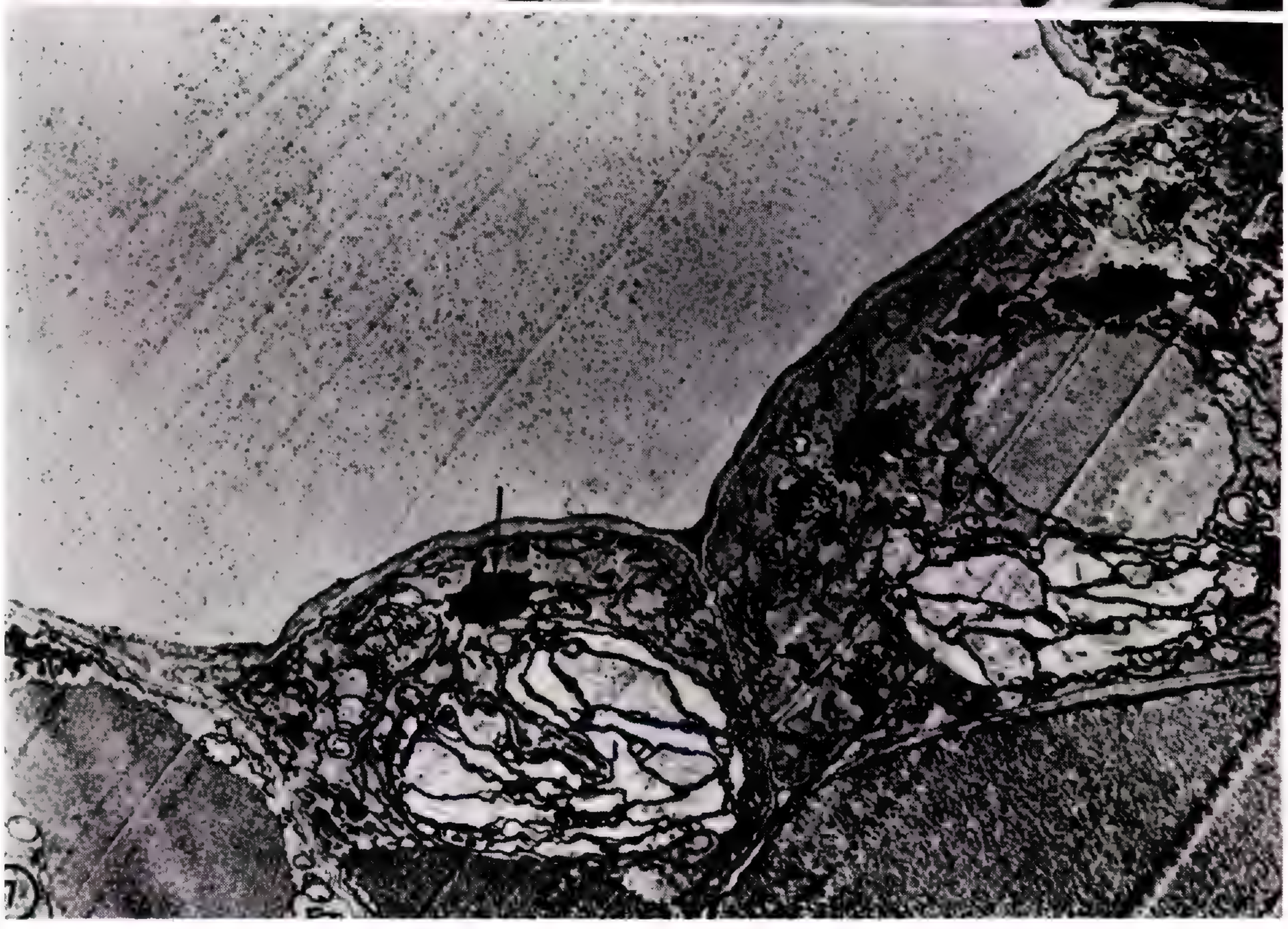


Fig. 5. Photomicrograph of a portion of a colony within the thallus of *Anthoceros punctatus*. Note the small densely staining cells adjacent to the cavity and transections (arrow) of the "host" tubular cells which project into the algal mass, ×800. Fig. 6. Electron micrograph of a portion of an *Anthoceros* "host" cell within an endophytic colony of *Nostoc*. Note the densely staining vacuole, the abundant mitochondria, elements of endoplasmic reticulum, and the plastid, ×14,400, $KMnO_4$ fixation. Fig. 7. Electron micrograph of a transection of the wall lining a developing mucilaginous cavity which has not yet been infected with *Nostoc*. Note the small cell size, the densely staining vacuoles (arrow), the numerous mitochondria, and elements of endoplasmic reticulum, ×7100, $KMnO_4$ fixation.

organelles were more numerous (possibly because of smaller cell size); and the plastids contained fewer internal elements as compared to those in thalloid cells not in contact with the cavity. Further ultrastructural studies utilizing the more recently developed aldehyde-fixation procedures may provide additional significant information with respect to the biotic relationship between the endophytic alga and its host. The algal cells generally were poorly fixed by the ultrastructural techniques employed. Further studies which are currently underway should provide further data with respect to the biotic relationship at the ultrastructural level.

Discussion

In each instance in which the algal isolate entered into the thalli and produced typical globose colonies and/or grew upon the substrate in intimate contact with the thalli, a significant difference in chlorosis between the experimental and control cultures was observed. The absence of the chlorotic conditions within the experimental plants indirectly suggests the ability of the blue-green algal isolates to fix atmospheric nitrogen and to provide an available source of nitrogen to the liverworts used in this experiment. These data do not support the conclusions of Pierce (1906). Additional studies for direct evidence of utilization of alga-fixed nitrogen are planned. In these experiments N^{15} will be used and the cultures will be grown in similar fashion with proper controls. Analyses for the presence of N^{15} within the thalli should provide direct evidence to support the above experiments.

Cytochemical and ultrastructural observations suggest that the biotic coaction between the liverwort and the blue-green alga may be also beneficial to the latter if the alga is capable of catabolizing the carbohydrate components of the mucilaginous matrix. In addition, Cobb & Meyers (1964) reported that in the blue-green alga *Anabaena cylindrica* nitrogen fixation is depressed by light intensities greater than those required to saturate photosynthesis. Their data show increased nitrogen fixation by the blue-green alga under light limiting conditions. That light intensity within the endophytic colony might be a limiting factor for photosynthesis and other photochemical events is suggested, firstly, by the lesser development of chloroplasts of thalloid cells which protrude through the algal mass, and, secondly, by the location of the cavity within the thallus as the cavity usually is covered by several layers of thalloid cells. Hence, if light is indeed limiting, nitrogen fixation by the endophytic alga would be enhanced.

Additional studies are needed to provide direct evidence of utilization of algal-fixed nitrogen, to define or isolate the algal influence which causes increased growth in cells surrounding the mucilaginous cavity, and to investigate the ability of the blue-green alga to utilize the carbohydrates of the cavity as a carbon energy source for metabolic activities under light limiting conditions. The present studies have shown that the biotic relationship between the blue-green alga and its liverwort host is, if not protocooperative, certainly beneficial to the hornwort host.

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THE GRAIN AMARANTHS AND THEIR RELATIVES: A REVISED TAXONOMIC AND GEOGRAPHIC SURVEY

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Much new information on this species group has accumulated in the years since my initial survey was carried out in the graduate laboratory of the Henry Shaw School of Botany (Sauer, 1950a). Many people have volunteered original field observations and collections from various places in Latin America, Asia, and Africa. Archaeologists have turned up the first material evidence of pre-Columbian grain amaranth cultivation in North America (Bohrer, 1962). Gradually, incidental to other work, I have had chances to study historically important collections in major European herbaria. Experimental plantings have answered some questions about variation patterns. Several long-standing taxonomic problems can now be resolved, classification simplified, and nomenclature corrected.

To make the revised presentation intelligible by itself, some information will be reviewed briefly, but without repeating details or documentation. The previous survey should be consulted for historical geography of the grain crop and for descriptions, illustrations, and lists of exsicattae of all the species. Sources will be cited for all newly presented information. Specimen citations for the new maps of the grain crop are given in the Appendix.

In both text and Appendix, references to specimens are accompanied by notations of herbaria in which they are deposited, according to the Index Herbariorum of the International Association for Plant Taxonomy.

THE GENUS AMARANTHUS IN RELATION TO MAN

Amaranths were widely distributed through the world's temperate and tropical regions even before man converted some of them into cosmopolitan weeds and domesticates. About 60 species were native to the Americas and a total of about 15 others to Europe, Asia, Africa, and Australia. Most were pioneer annuals of naturally open habitats: mountain and desert canyons, riverbanks, lakeshores, tidal marshes, and ocean beaches. Producing abundant seed that is widely dispersed by water and birds, they survived by constant colonization of sites with

[1] I am indebted to all the people referred to in the text who supplied unpublished information, photographs, and new collections. Many of these contributions were inspired by Edgar Anderson and were relayed through the Missouri Botanical Garden. A special Guggenheim Foundation grant to Professor Anderson made possible massive experimental plantings, conducted by George Freytag at the Escuela Agricola Panamericana, Zamorano, Honduras; these provided adequate population samples grown under uniform and favorable conditions. I am also indebted to the curators of the herbaria and museums cited for making their indispensable collections available for study. Vorsila Bohrer and Joel Andress supplied useful ideas and leads to sources of which I was unaware. The maps were prepared by Jeanne Tsou Liu in the University of Wisconsin Cartographic Laboratory, under the direction of Randall Sale.

disturbed soil, full sun, and little competition. Long natural selection for such a way of life preadapted certain of the species for success in habitats drastically disturbed by man.

The beginnings of their association with man may be cryptically recorded in pollen deposits, but palynology can not yet discriminate amaranth pollen from that of related plants. Even before the origins of agriculture, some amaranths must have flourished around camps and fishing villages. Prehistoric peoples undoubtedly used these conveniently available volunteers in several ways.

Any amaranth seeds, so far as is known, are quite edible when simply toasted and milled, tasting much like true cereals. Analyses and nutrition experiments show the grain to be comparable to true cereals as carbohydrate food and superior in protein and fat content (Hunziker, 1952, p. 78; Singh, 1961, pp. 3-5). Though the seeds average only about 1 mm in diameter, they are obtainable in prodigious quantities, even by primitive gathering techniques (Jones, 1953, p. 90). There are innumerable historical and ethnographic accounts of such gatherings in many regions. Archaeologic amaranth seeds, often in massive caches, are associated with such diverse cultures as Lake Dweller in southern Europe (Thellung, 1914, p. 327), Hopewellian in the Illinois Valley (Struever, 1964, p. 102), Basketmaker in Colorado (Jones & Fonner, 1954, p. 94), a pre-ceramic old dune hearth in New Mexico (Agogino & Feinhandler, 1957, pp. 154-155; Agogino & Hester, 1958, p. 187), and incipient agricultural levels in Tamaulipas and Puebla caves (Kaplan & MacNeish, 1960, p. 36; MacNeish, 1964, p. 534). The species involved are not known, but it seems likely that whatever amaranths were locally available were gathered indiscriminately. Domestication of selected species as grain crops was concentrated in definite regions of the New World, as will be shown below.

Young amaranth leaves and shoots are boiled as greens or potherbs in much of the world. Generally, volunteer weeds are gathered with little discrimination as to species. Careful selection as potherbs leading to domestication evidently took place only in Asia. A variety of cultivated races assigned to *Amaranthus lividus* L. and *A. tricolor* L. (both s.l.) are common potherbs of eastern and southern Asia; these have been introduced to the western world under such names as Chinese spinach, Malabar spinach, and *tampala*, the generic name for amaranths in Ceylon. The American grain amaranths make good potherbs and one is now widely planted as such in the Old World. In their native regions, thinnings from the grain crops are often salvaged as boiled greens but they do not seem to be planted for that reason nor even preferred to their weedy relatives.

Many wild amaranth species have quite noticeable and variable red coloration of inflorescences, leaves, and stems, due to an anthocyanin of the type found in beets. Such pigmentation is intensified in certain forms of all the domesticated grain and potherb species. Selected deep red forms, closely related to some of those grown for grain, are widely scattered as ceremonial, magical, and simply ornamental plants.

Although many amaranths have some role in culture history, a few New World species stand out as especially significant. These belong to a single section (*Amaranthus*) of the genus, with which the rest of this paper is solely concerned.

Chacteristics of Amaranthus sect. Amaranthus

This section includes all the domesticated grain and dye amaranths, most of the domesticated ornamentals, and most of the common weeds. It has long been recognized as a section under the name *Amaranthotypus* Dumort (Thellung, 1914, p. 230; Sauer, 1950a, p. 594; Grant, 1959b, p. 319; Aellen, 1961, p. 467). Under the present rules of nomenclature, it must bear the same name as the genus, since it includes the type species, *A. caudatus* L. Members of the section form a coherent group, perhaps close to the primitive core from which other sections of the genus radiated.

The section is distinguished from the bulk of the genus by the following combination of characters: plants monoecious; cymes continuing above uppermost leaves to form large, compound terminal inflorescences; tepals and stamens 5 (or varying between 3-5 in flowers of the same plant); utricle circumscissile (indehiscent in occasional mutant and hybrid individuals). As a rule these characters are extremely constant (the parenthetically noted variants are mainly within one species, *A. powellii.*)

Some of the sectional characters are clearly connected with the success of its members as grain crops: the monoecious habit, the dehiscent utricle allowing easy threshing and winnowing, and the large compound inflorescences producing enormous quantities of seed. Estimates of seed production of individual plants in this group have usually been on the order of several tens of thousands, but yields of over 500,000 seeds from a single plant of *A. retroflexus* have been reported (Priszter, 1950, p. 81).

Within the section, discontinuities between species are, as a rule, quite clear-cut. The group has an undeserved reputation of being taxonomically difficult, mainly because of hopeless attempts to recognize taxa by pigmentation, which segregates within populations, and by growth form, which is extremely plastic under different day lengths and other environmental variables. There are abundant constant characters, particularly in shapes and proportions of pistillate flower parts, whose correlated discontinuities reveal genetically isolated species.

However, breeding barriers between the species are by no means always absolute, even when species have different chromosome numbers[2]. An imposing array of hybrids, involving most of the members of this section, have been reported in the literature, recently reviewed by Grant (1959b, p. 321) and Aellen (1961, pp. 512-514). The importance of these hybrids can easily be exaggerated because many are sterile or rapidly eliminated by natural selection. However, some weedy and cultivated populations have variation patterns suggesting effective introgression; these will be noted under the species involved.

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[2] Chromosome counts have so far been of little help in amaranth taxonomy, except in the polyploid *A. dubius* (Grant, 1959a, p. 1064). Diploid numbers of 32 or 34 have been found in all the many other species studied (Grant, 1959b, pp. 315-319). Both counts have sometimes been reported for the same species and the difference shows no apparent connection with relationship or crossability.

a. Bract much shorter than tepals.
  b. Tepals acute, shorter than utricle ..... *A. brandegei*
  bb. Tepals obtuse or retuse, longer than utricle.
    c. Tepals retuse ..... *A. celosioides*
    cc. Tepals obtuse ..... *A. pallidiflorus*
aa. Bract equalling or exceeding tepals.
  b. Tips of tepals incurved against utricle; bract and all tepals approximately equal in length.
    c. Lower cymes pistillate, upper staminate; spines in leaf axils ..... *A. spinosus*
    cc. Each cyme with initial staminate flower and remainder pistillate; plants unarmed ..... *A. dubius*
  bb. Tips of tepals straight or spreading away from utricle; inner tepals definitely shorter than outer tepals and bract.
    c. Utricle much shorter than tepals; seed less than 1 mm in diameter.
      d. Inflorescence very large, much branched; outer tepals obovate ..... *A. scariosus*
      dd. Inflorescence small, unbranched; outer tepals spatulate ..... *A. bigelovii*
    cc. Utricle equalling or exceeding some or all tepals; seed at least 1 mm in diameter.
      d. Inflorescence short, unbranched; style-branches longer than utricle ..... *A. viscidulus*
      dd. Inflorescence large, branched; style-branches shorter than utricle.
        e. Inflorescence branches short and thick; tepals all retuse or obtuse ..... *A. retroflexus*
        ee. Inflorescence branches long or slenger or both; outer tepals acute or acuminate.
          f. Fully developed inflorescence moderately large; bract exceeding style-branches; seed dark brown (PROGENITORS OF THE DOMESTICATED SPECIES—coarse, weedy plants, generally green with dull red pigmentation).
            g. Inflorescence stiff, with few branches; bract about 5 mm long, with extremely heavy midrib; style-branches thick at base; tepals and stamens 3 to 5 ..... *A. powellii*
            gg. Inflorescence lax, usually with many branches; bract 3 to 4 mm long, with moderately heavy midrib; style-branches slender at base; tepals and stamens 5.
              h. Tepals straight, the inner oblong, acute ..... *A. hybridus*
              hh. Tepals recurved, the inner spatulate, obtuse ..... *A. quitensis*
          ff. Fully developed inflorescence enormous; bract not exceeding style-branches; seed dark brown or pale ivory, often tinged with red in *A. caudatus* (DOMESTICATED SPECIES—attractive, cultivated plants, generally bright green or intense red or various striking combinations).
            g. Inflorescence stiff; bract equalling style-branches, with moderately heavy midrib; style-branches thick at base ..... *A. hypochondriacus*
            gg. Inflorescence lax; bract not exceeding utricle, with slender midrib; style-branches slender at base.
              h. Tepals straight, the inner oblong, acutish; style-branches erect ..... *A. cruentus*
              hh. Tepals recurved, the inner spatulate, obtuse or emarginate; style-branches spreading ..... *A. caudatus*

Wild Species

Of the 12 wild species listed in the key, the first nine will be passed over briefly; their taxonomy has remained comparatively unconfused and they are not believed to be directly related to the grain species.

Amaranthus brandegei Standley, *A. bigelovii* Uline & Bray, and *A. viscidulus* Greene are minor, non-weedy endemics of the southwestern U.S. and northwestern Mexico.

Amaranthus scariosus Benth. is common and weedy in southern Mexico and Central America, but has not emigrated to other regions.

Amaranthus celosioides H.B.K. has been found at scattered places in western South America from Venezuela and Colombia to Chile, on the Galapagos, and on San Lorenzo Island off Peru. Specimens are few and rather heterogeneous.

Amaranthus pallidiflorus F. Muell. is the only member of the section native to the Old World. It is known only in Australia, except for ephemeral adventives introduced with Australian wool. I have seen it in quite natural habitats on the coastal dunes of Western Australia. The least incredible origin would seem to be by ancient, long range dispersal from South America[3].

Amaranthus spinosus L. and *A. dubius* Mart. ex Thell. are the commonest and most widespread weedy amaranths of the New World tropical lowlands, where they presumably originated. *Amaranthus dubius*, the only known polyploid amaranth species, is probably an allotetraploid to which *A. spinosus* contributed one chromosome set (Grant, 1959a, p. 1068); the other progenitor is evidently either *A. quitensis* or *A. hybridus*. By 1700, *A. spinosus* was spreading rapidly through the warmer parts of the world, both as a weed and as a sporadically planted potherb. *Amaranthus dubius* followed more slowly, being found at only a few places in the Old World before 1800; it has not spread as widely as *A. spinosus* outside the tropics. Sterile hybrids between the two are common, and have elicited some Latin names, e.g. *A. caracasanus* H.B.K.

Amaranthus retroflexus L. is a native riverbank pioneer of the central and eastern U.S. and adjacent regions of southeastern Canada and northeastern Mexico. In much of this area it has become one of the commonest of all agricultural weeds and thus is often mistaken for an exotic. Peter Kalm sent seeds from Pennsylvania to Linnaeus; the progeny grown at Uppsala, some of which are preserved (LINN 1117.22), may have been the first in Europe. Thellung (1914, p. 258) blamed Linnaeus for inoculating Europe with the species by disseminating it to botanical gardens. By 1800, it was becoming a common weed through much of the continent (Priszter, 1951, p. 261) and soon after spread into the Near East and North Africa. It has since become naturalized throughout temperate regions of the northern and southern hemispheres. In areas of overlap with *A. powellii* and *A. hybridus*, *A. retroflexus* forms many partially sterile hybrids, especially in weed populations of highly artificial habitats.

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[3] A similar enigmatic disjunction occurs between South American and Australian coastal populations of *Carpobrotus* (*Mesembryanthemum*).

The other three wild species will be considered in more detail, as they appear to be directly related to the domesticated grain species. Their taxonomy and nomenclature have been appallingly confused, mainly by attempts to classify continuous intraspecific variations. Synonymy will be limited to basionyms of recently used names.

Amaranthus powellii S. Wats., Proc. Amer. Acad. **10:** 347, 1875.

Type: United States, grown at Harvard Univ, 1874, seed obtained from Arizona Indians by *Powell s.n.*, US 16163; isotype MO.

A. chlorostachys Willd. var. *pseudoretroflexus* Thell., Vierteljahrsschr. Naturf. Ges. Zürich **52:** 443, 1907.

Type: Switzerland, Derendinger, Solothurn, by worsted yarn factory, 1907, *Probst s.n.* (not seen, but Thellung's description is diagnostic).

A. bouchoni Thell., Monde des Plantes, sér. 3, **45**(160): 4, 1926.

Type: France, Bordeaux, trash dumps by harbor, 25 Sept. 1925, *Bouchon s.n.*, fragment US (Thellung published simultaneously an alternative name *A. hybridus* subsp. *hypochondriacus* var. *chlorostachys* subvar, *genuinus* f. *bouchoni*).

Amaranthus powellii is a pioneer of canyons, desert washes, and other open habitats, ranging through the western Cordilleran system of North and South America, with wide gaps in the wetter regions of Central America. The species has long been a common weed in the West. It began appearing as a rare adventive in eastern North America about 1900; since 1940 it has become a widespread and troublesome weed there. The species also arrived in Germany as an adventive shortly before 1900 and has since become an abundant and still expanding weed of northern and central Europe, where it is usually misidentified as *A. chlorostachys* Willd., a synonym of *A. hybridus*. It has also recently invaded southern India and South Africa.

The species is exceptional in producing flowers with tepal and stamen numbers varying from 3 to 5, even on a single plant. Also, individual plants with indehiscent utricles occur sporadically in native American populations and have formed whole local populations in Europe (Brenan, 1961, p. 270; Aellen, 1961, p. 475), where they have elicited the name of *A. bouchoni*. Such aberrant forms are common among hybrids between other species of *Amaranthus*, but in *A. powellii* they evidently arise without hybridization. The species is involved in partially fertile hybrid swarms in eastern North America, where it is invading territory of *A. retroflexus* and *A. hybridus*, in western North America where the converse is true, and in Europe, where all three are recent immigrants. It also crosses locally with the domesticated grain species, as noted below.

Amaranthus hybridus L., Sp. Pl. 990, 1753.

Linnaeus' phrase-name, *A. racemis pentandris cylindricis horizontalibus, caule inermi*, and the geographic source, Virginia, are appropriate but inconclusive. He also gave two synonyms: (1) *A. sylvestris maximus novae angliae, spicis viridibus*, attributed to John Ray (1686-88, **1:** 201), but Ray's name ended

with . . . *spicis purpureis, carneis, aut viridibus,* and Linnaeus was actually following Tournefort (1719, **1:** 235) in dividing Ray's species into three according to inflorescence color; (2) *A. major, virentibus spicarum paniculis, semine nigro* Barr. (Barrelier, 1714, *fig.* 648). Barrelier's drawing is a fair likeness of the species and all the material available for typification agrees: a specimen bearing Tournefort's polynomial in the Hortus Cliffortianus herbarius (BM), a Clayton specimen from Virginia bearing the same name in the Gronovius herbarium (BM), a specimen labelled *A. hybridus* from the Uppsala Botanic Garden (LINN 1117.19).

A. chlorostachys Willd., Hist. Amaranth. 34, *tab. 10, fig. 19,* 1790.
The only specimen labelled *A. chlorostachys* in the Willdenow herbarium is a collection by *Hermes B 17521.* It agrees well with the (ambiguous) description and plate.

A. patulus Bertol., Comment. It. Neap. 19, *tab. 2,* 1837.
Based on plants found by Bertolini in the plain of Pascone, nr Naples, Italy, which are not known to have been preserved.

A. incurvatus Tim. ex Gren & Godr., Prosp. Fl. France 8, 1846.
Type: France, Tigneu nr Lyon, *Timeroy s.n.* (not seen, but original description fairly diagnostic).

Amaranthus hybridus is evidently a native riverbank pioneer of milder and moister regions from eastern North America through Mexico and Central America to northermost South America. It has long been a common field weed in this region. Its earliest and most successful emigration was to the Mediterranean region, where it arrived by the early 18th century and became abundant during the 19th century. The species has appeared repeatedly but ephemerally in northern Europe. It has recently become a naturalized weed in western North America, eastern Asia, Australia, and South Africa. At home and abroad, wherever weed populations of *A. hybridus, A. powellii,* and *A. retroflexus* mix, partially fertile hybrids appear. Hybrids with the domesticated *A. hypochondriacus* and *A. cruentus* are discussed below.

AMARANTHUS QUITENSIS H.B.K., Nov. Gen. Spe. Pl. **2:** 194, 1817.

Type: Ecuador, banks of Río Guallabamba, alt ca 2000 m, June 1802, *Humboldt & Bonpland 156* (not seen, but the original description is diagnostic).

Amaranthus quitensis is evidently a native riverbank pioneer of South America, both in the mountains of the northwest and at lower elevations in the temperate south. It is also present in the Galapagos, perhaps naturally. Throughout much of South America, the species has become the commonest weed amaranth. It is not known to be naturalized elsewhere, although it has appeared repeatedly in Europe since the late 19th century as an ephemeral adventive, especially around ports and woolen mills.

Forms of this species with stout, intensely red inflorescences grow in Andean gardens and maize fields from Ecuador to northwest Argentina. Called *ataco* or *sangorache,* the plants are semi-cultivated or tolerated as volunteers useful in

coloring *chicha* and ceremonial maize dishes (Sauer, 1950b, p. 412; Heiser, 1964, pp. 137-139). It is not known whether such use is ancient; the earliest available collections are modern (e.g. Peru, Torontay, *jataco achihuite,* 1915, *Cook & Gilbert 1893,* US; Ecuador, nr Huigra, *ataco, sangorache,* 1918, Rose 22145, US). In aspect the plants look suspiciously like domesticates such as *A. cruentus,* which is used to color ceremonial maize bread in North America. However, if these plants are derived from hybrids between domesticated and weedy amaranths, backcrossing to the weedy *A. quitensis* has obliterated any clearly diagnostic characters of the other species. Another possibility is that the plants are pure *A. quitensis* in a stage of incipient domestication.

Domesticated Species

The three grain species diverge from their closest wild relatives in several similar ways. Bracts are relatively short and weak, perhaps because of selection favoring inflorescences that are less prickly when rubbed between the hands, a common method of extracting the grain. Plants and inflorescences are extremely large, giving greater grain yield with little or no increase in seed size. Pale ivory seeds, preferred for popping quality and flavor, predominate in the grain crops of all three species. The wild type dark brown seeds, characteristic of all other amaranths, are produced by some plants in most grain crops. In the absence of constant artificial elimination, the dark seed type may have the advantage, judging from its frequency among feral plants and those cultivated for non-grain purposes.

The nomenclature of these three fairly coherent and discrete species has been complicated by giving different Latin names to some of the more conspicuous variants that constantly appear within each population and then multiplying these names by shifting them up and down the taxonomic hierarchy. Only partial synonymy will be given, emphasizing basionyms of commonly used names.

Amaranthus hypochondriacus L., Sp. Pl. 991, 1753.

The phrase-name, *A. racemis pentandris cylindricis erectis, caule inermi,* is appropriate for this species but rather ambiguous, and the source, Virginia, is implausible. Linnaeus referred the name to his Hortus Cliffortianus of 1737 and Hortus Upsalensis of 1748, where it had been associated with synonyms that Linnaeus transferred to *A. hybridus* in the Species Plantarum. Probably the notation of Virginia should have gone along in this transfer but was left behind as a relic of former lumping of the two species. The only synonym given for *A. hypochondriacus* in the Species Plantarum is *A. sylvestris maximus novae angliae, spicis purpureis* Tournef. (Tournefort, 1719, **1:** 235), a name of uncertain meaning derived by splitting a species of Ray (1686-88, **1:** 201) that was mainly if not entirely *A. hybridus.* The literature thus establishes that Linnaeus recognized a species similar to *A. hybridus* but distinguishable by its more erect and more intensely colored inflorescences. This hazy distinction becomes clear enough in the presence of a Linnaean herbarium specimen labelled *A. hypochondriacus* (LINN 1117.24).

A. flavus L., Syst. Nat. ed. 10. **2:** 1269, 1759.
The original description and a longer one in the 1763 edition of the Species Plantarum are ambiguous. In the latter, the source is given as India. Fortunately there is a Linnaean herbarium specimen labelled *A. flavus* (LINN 1117.23).

A. frumentaceus Buch.Hamilt. ex Roxb., Fl. Ind. **3:** 613, 1832.
Buchanan-Hamilton originally applied his unpublished name to a grain crop, called *kiery,* he discovered on the hills of South India between Mysore and Coimbatore, where *A. hypochondriacus* is still a common crop under the same name. Roxburgh's description of the species was at least partly based on a large patch of amaranths planted in the East India Company's Botanical Garden, Calcutta. A specimen labelled *A. frumentaceus* in Roxburgh's herbarium (K) was designated by Sir E. J. Salisbury as the probable type, according to Hunziker (1952, p. 68).

A. anardana Buch.-Hamilt. in Wall. ex Moq.-Tand. in DC., Prodr. **13**(2): 256, 1849.
Type: Bhagulpur and Nepal, *Wallich 6903,* Moquin-Tandon herbarium, P; possible isotype: Bhagulpur, Bihar, 2 Nov 1813, *Buchanan-Hamilton 2028-1,* E. In Wallich's catalogue, under 6903, *A. anardana* appeared as a nomen nudum, with collections listed from Bhagulpur, Beloya, and Nepal, 1821. There is no evidence that the Beloya collection was included in Moquin-Tandon's treatment, which is fortunate because it is probably *Buchanan-Hamilton 2028-2* belonging to *A. caudatus.*

A. hybridius L. (var) *γ erythrostachys* Moq-Tand. in Dc., Prodr. **13**(2): 259, 1849.
Type: France, seed from Montpellier Bot Gard grown in Toulouse Bot Gard, 17 Sept 1844, Moquin-Tandon herbarium, P.

A. leucocarpus S. Wats., Proc. Amer. Acad. **10:** 347, 1875.
Type: United States, grown at Harvard Univ, 1874, seed obtained from Arizona Indians by *Powell, s.n.*. US 15163; isotypes GH, MO, US.

A. leucospermus S. Wats., Proc. Amer. Acad. **22:** 446, 1887.
Hyponym for *A. leucocarpus.*

Amaranthus hypochondriacus was evidently derived mainly from *A. powellii* by selection as a grain crop within the great region of its aboriginal cultivation in North America. Its distribution as a grain crop in Asia, although perhaps old, is clearly secondary and its wide dispersal as an ornamental is recent.

There has been at least local genetic admixture from another domesticate, *A. cruentus,* and its progenitor, *A. hybridus.* Active hybridization is surprisingly limited considering the great geographic overlap with close relatives. In Mexico both *A. powellii* and *A. hybridus* are common weeds of the *A. hypochondriacus* grain crop, and traces of the domesticate are easy to find in the weed populations. The effect of backcrossing to the crop is probably limited by the fact that hybrids mostly produce dark seeds that are rejected for planting. An exceptional case occurs in a highly aberrant race from Los Reyes, Michoacan, grown to make special black *tamales* and unique among Mexican grain amaranths in being entirely dark seeded (Appendix); this appears to be a stabilized hybrid between *A. hypochondriacus* and *A. hybridus.* In pale seeded grain crops, weed introgression is comparatively subtle, the clearest known case being in a Warihio Indian crop from Rancho Trigo, Chihuahua (Appendix); progeny raised from this grain are heterogeneous and some individuals definitely resemble *A. powellii.* In southern Mexico, particularly Oaxaca, local populations of *A. hypochondriacus* show some resemblances to *A. cruentus,* which is also planted there as a grain crop; similar atypical plants appear in the *A. hypochondriacus* grain crop of Madras, India, where *A. cruentus* has also been introduced (Appendix). Arizona Indian crops of *A. hypo-*

chondriacus, especially a dark seeded archaeologic specimen, may also show traces of introgression from *A. cruentus*, but the resemblance is too faint to be sure.

Amaranthus hypochondriacus as a New World Grain Crop (*Fig. 1*).

In Arizona, well preserved inflorescences and seeds of the species were recently excavated in a cliff-dwelling at Tonto National Monument (Univ of Michigan, Ethnobotanical Laboratory *4024A* & *4038*—both pale seeded; *4029*—dark seeded; deposited at Southwest Archeologic Center, Globe, Arizona; fragments WIS). The occupation, dated at 1350 to 1400 A.D., was by Salado Indians practicing irrigated agriculture with maize, beans, and squash. Their culture was an amalgamation of Hohokam and Anasazi; earlier Hohokam cultivation of grain amaranths is suggested by large caches of charred seeds of an undetermined *Amaranthus* sp. (Bohrer, 1962, p. 108).

There are hints that the crop may have persisted in this region until recently. About 1890, the custodian of Casa Grande ruin (Whittemore, 1893, p. 52) was told by the Pima that a hundred years before, when they lived some miles west of Casa

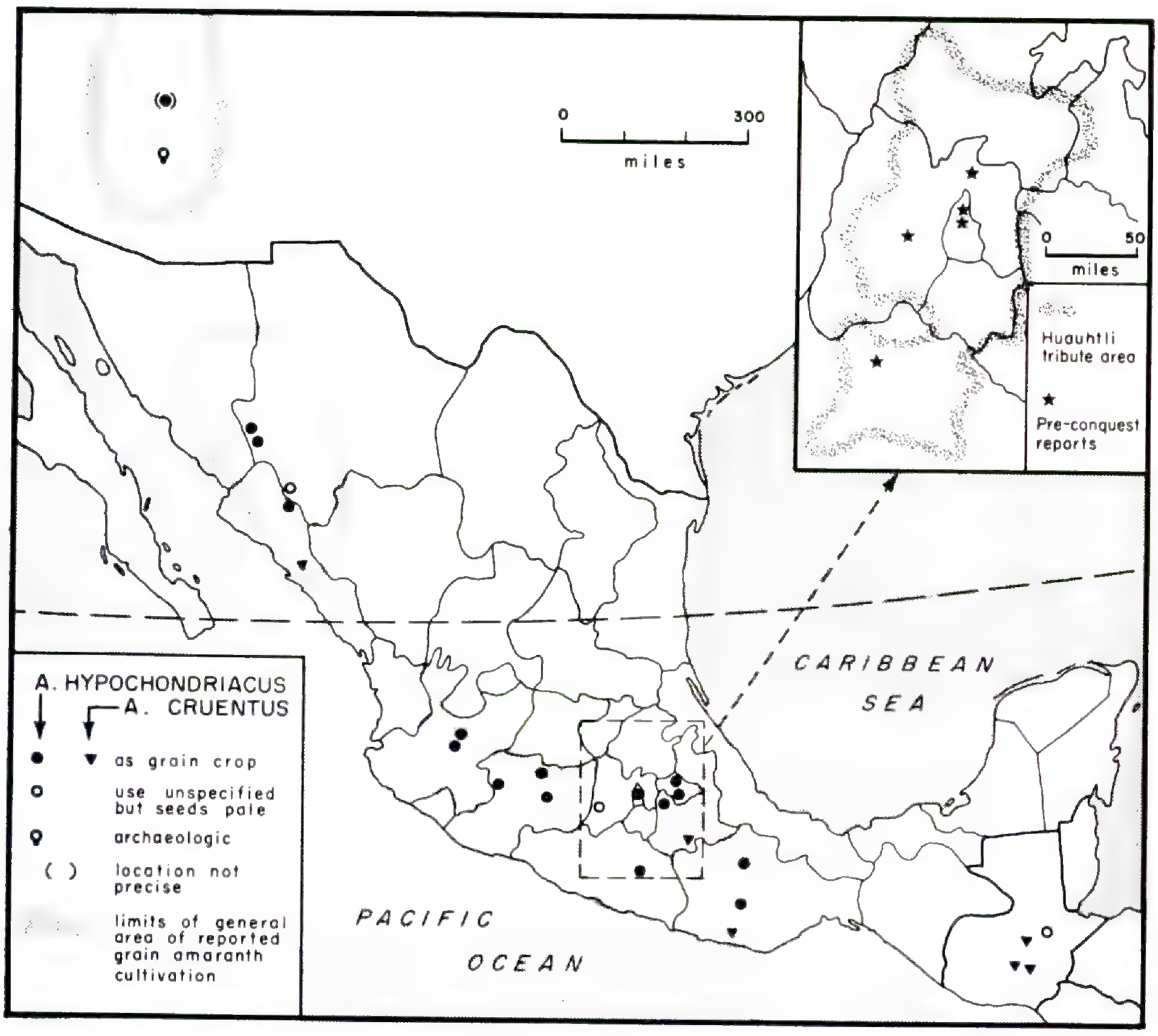

Fig. 1. North American distribution of grain amaranths. Inset: pre-Conquest localities reported and provinces giving tribute of the grain to Moctezuma.

Grande, "they raised cotton, corn, melons, and pumpkins, and a small round seed which they ground and boiled as mush." This may be connected with a report by Russell (1908, p. 74) that the Pima used an unidentified annual plant called *ki'ak,* whose seeds were popped like corn and ground on the metate.

The only tangible historic records of the species among the Arizona Indians are from farther north. Major Powell's mixed bag of domesticated and wild amaranth seeds, from which the types of *A. powellii* and *A. hypochondriacus* were grown, was probably collected during his stay with the Paiute; at any rate, Edward Palmer, who was also with the Paiute in the 1870's, reported they cultivated the latter and milled the seeds for bread and mush.

In Mexico, much of the early history of the grain amaranth crop depends on common names. At the time of the Conquest, the Nahua name *huauhtli* was widely used for both amaranths and chenopods, including those used as potherbs; however, *A. hypochondriacus* was probably the main if not the only species cultivated for grain. The paste made from the milled *huauhtli* grain was generally called *zoale.* In several Indian languages of northwestern Mexico, the same crop was called some variant of the word *guegui.* Beginning in the 17th century, the Spanish name *alegria* was applied to confections of popped amaranth grain and was gradually extended to the plants that produce it; the plants have also commonly been called *bledo,* the Spanish name for amaranths in general.

In the northwestern Sierra Madre during the colonial period, the Jova and Tarahumare Indians grew pale seeded grain crops under names similar to *guegui,* identified in Spanish with *zoale* or *alegria.* The grain was used much like maize, popped or toasted and milled. In 1953, Brugge (1954, personal communication) found *guegui* cultivated for *pinole* near the Tarahumare pueblo of Metate in Sinaloa and was told that it is still grown in the mountains of southern Sonora. The Mayo, Warihio, and Tepehuan Indians grow pale seeded *A. hypochondriacus* in the same general region under the name *guegui, huauhtli, bledo,* or variants (Appendix). Among the Yaqui in Sonora, Spicer (1954, p. 49) was told by the old people that amaranth seeds, called *we'e,* were formerly ground and used much like maize; they remembered the food as a delicacy that was presented to the spirits of the dead in All Soul's Day ceremonies; Spicer reported the seeds were black and were gathered from wild plants, but the name and ceremonial use suggest some traditional connection with the *A. hypochondriacus* crop. In the 19th century farther south in the Sierra Madre of northern Jalisco, the Huichol Indians cultivated a pale seeded amaranth called *wā-vë* that was almost certainly of this species; they milled the grain to make little cakes shaped like animals which played a central role in their greatest annual ceremonial.

In the tropical highlands of central Mexico, *huauhtli* was a major grain crop at the time of the Conquest. Moctezuma collected *huauhtli* tribute totalling about 200,000 bushels a year, nearly equal to maize tribute, from 17 provinces of the Aztec Empire (Fig. 1). During the 16th century, the crop was recorded as a traditional staple in the same region and far beyond, from Jalisco in the west to Oaxaca in the east. The grain was toasted, milled for *zoale,* made into tortillas, rolled into little balls, or powdered and drunk as *atole.*

Fig. 2. Ripening field of *A. hypochondriacus* grown for making *alegrias,* nr San Gregorio Atlapulco, D. F., Mexico. [Photo R. C. West]

Fig. 3. Young field of *A. hypochondriacus,* same area as Fig. 2. Photo [J. D. Sauer]

Among the Aztecs and their neighbors, the grain had unique religious importance. Idols of *zoale* were the centers of innumerable little household rituals and of the greatest state ceremonies and processions. Far to the south in Oaxaca, the grain evidently also had special significance for the late prehistoric Mixtecs; the famous Tomb 7 at Monte Alban contained a human skull encrusted with turquoise mosaic; the mosaic was set in a paste originally thought to be copal gum (Caso, 1932, p. 510) but shown by later analysis to be *zoale* (Caso, 1966, personal communication).

In Christian eyes the Mexican grain amaranth was the very symbol of heathen idolatry and its cultivation declined drastically during the colonial period. However, even in the valley of Mexico, pagan rituals involving *zoale* persisted into the 17th century. Rosaries with the beads made of *zoale* paste appeared in the late 19th century.

Amaranthus hypochondriacus is still grown here and there through the ancient *huauhtli* area, ordinarily in small patches near houses or in maize fields. The grain is still used as an ordinary food in scattered places, parched and milled much like maize; by far the commonest use nowadays is for *alegria* confections, like little popcorn balls bound with syrup, which have become traditional for certain festivals and saints' days.

There are only a few new records of the crop in central Mexico. In 1962, *alegria* cakes were common in the market at Tehuacán, Puebla (Whitaker & Cutler, 1966, p. 11). West (1966, personal communication) found a small plot of grain amaranths in the old Indian town of Oaxaca near Monte Alban and also saw *alegrias* on sale in the Tlacolula market nearby. Scattered fields of *A. hypochondriacus* have been maintained in the Xochimilco area (Fig. 2-3) to supply *alegrias* for the Mexico City market; some plantings are in *chinampas*, the so-called floating gardens, where legends recorded in the 16th century placed *huauhtli* cultivation before the Conquest.

Amaranthus hypochondriacus as an Old World Grain Crop (Fig. 4-5).

For at least a hundred years, the species has been a far more widespread and important crop in Asia than in its homeland. Early botanists and explorers generally took it for an indigenous domesticate because it was so well established in subsistence agriculture, more often than not in remote regions. There are, of course, other American Indian crops that followed the same pattern, including the Andean *Amaranthus caudatus* L. and perhaps *Chenopodium quinoa Willd.* A tall chenopod of uncertain identity which strongly resembles the latter has long been grown as a grain crop in the hills of northwest India, where it shares the name *bathu* with grain amaranths (Thomson, 1852, p. 49; Singh, 1961, p. 40).

The first known record of *A. hypochondriacus* in Asia was Linnaeus' description of a form from India under the name *A. flavus*. Later in the 18th century, just before the end of the Dutch period in Ceylon, Koenig collected a pale seeded specimen there under a Sinhalese name meaning seed or grain amaranth (Appen-

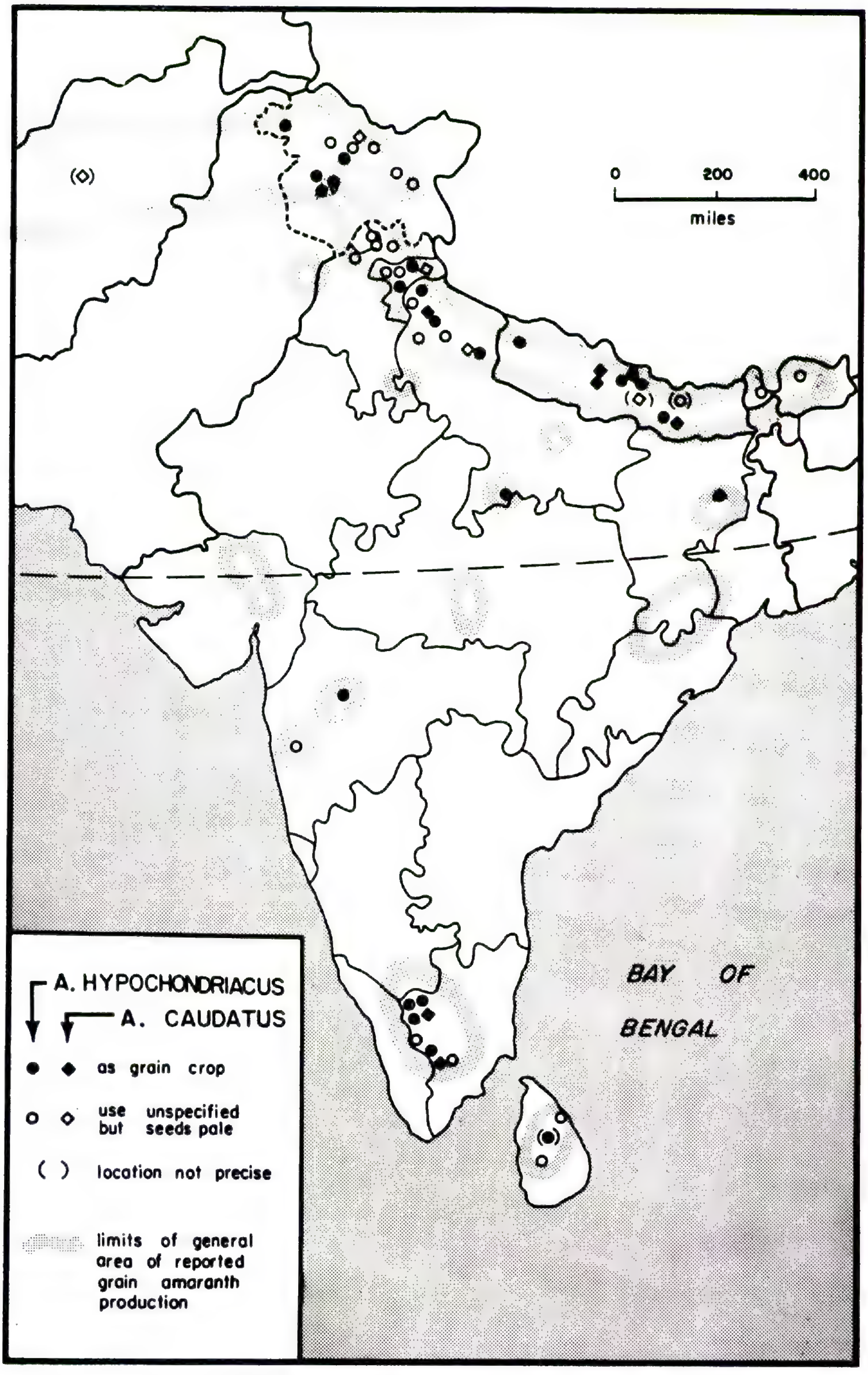

Fig. 4. Grain amaranth distribution in India and adjacent regions.

dix). In the 19th century, grain amaranths were also reported cultivated in Ceylon under the local name *landesi* (= *hollandesi?*).

During the early and mid 19th century, *A. hypochondriacus* was collected and recorded as a grain crop among the hill tribes of south India, in the Deccan plateau, and in the Himalaya; during the late 19th century it was found through interior China to eastern Siberia (Appendix).

Some important early Himalayan records were not noted in the previous survey (Sauer, 1950a). In the northwest, Vigne (1844, **1:** 36) stated that bread made from a grain of a crop called *batu* was a common food of Himalayan peasants; he identified the crop as a cockscomb or *A. cruentus;* it was almost certainly *A. hypochondriacus*. In 1833, Vigne saw red and yellow patches of the crop on hillsides at Serai near Simla; in 1835 he found it as a grain crop at Skardo and in 1838 in the valley of Kashmir (1844, **1:** 36, 309, **2:** 263). An amaranth had previously been noted among the grain crops of Kashmir by Moorcroft and Trebeck in 1823 (Wilson, 1841, **2:** 132). Some of the earliest collections of *A. hypochondriacus* from Kashmir and the Simla area of Himachal Pradesh were made by Thomson (Appen-

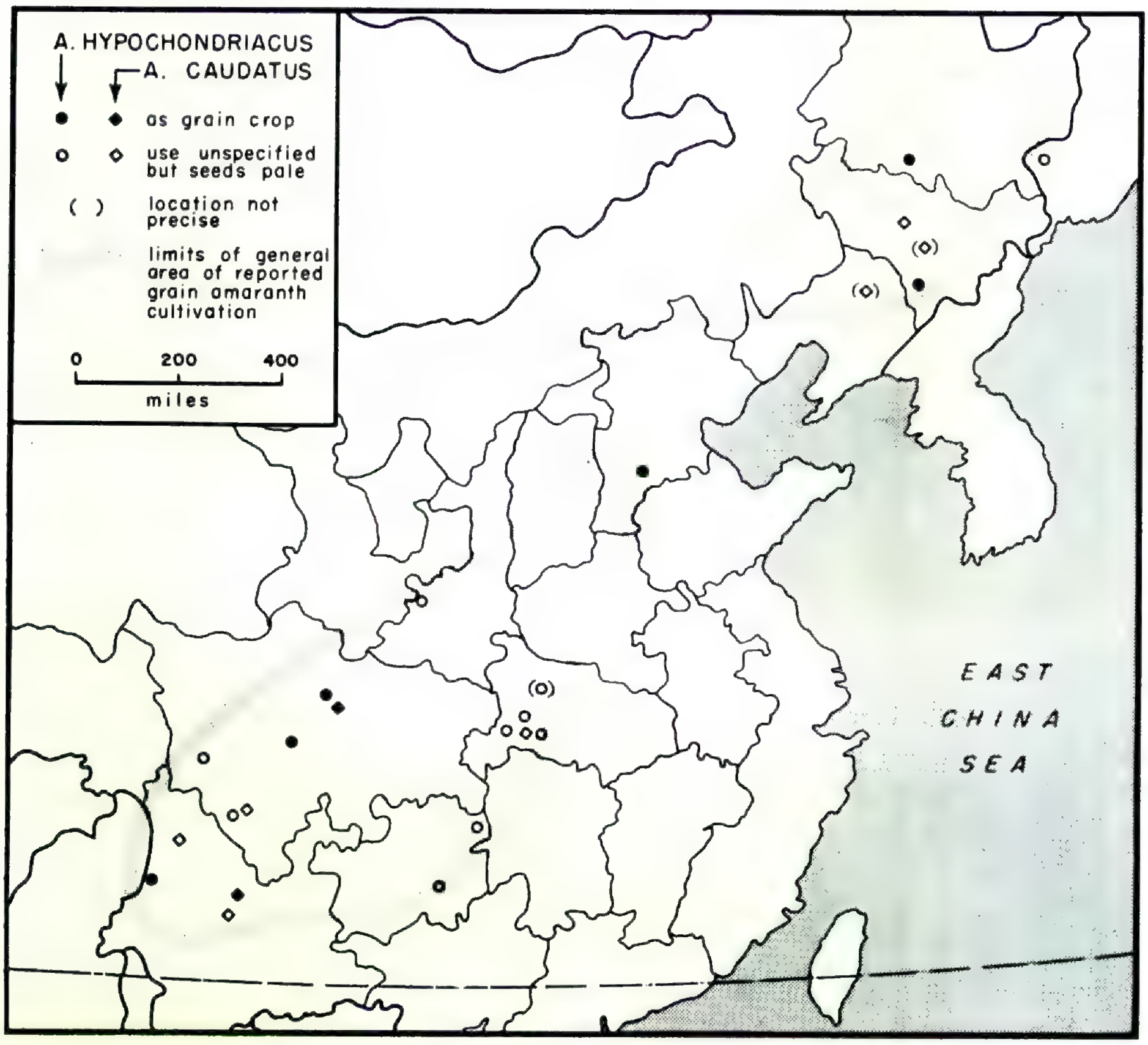

Fig. 5. East Asian distribution of grain amaranths.

dix). He wrote (1852, p. 49) that there were many fields of *Amaranthus* near Simla, on ridges above the Sutlej Valley, and that it was "occasionally cultivated in all parts of the hills, its bright red inflorescence, in autumn, tinging with flame the bare mountain slopes." Also near Simla, Markham (1854, p. 78) saw crops of *batu* clothing the cultivated spots with waving plumes of yellow and vivid crimson; he recognized *batu* as a kind of prince's-feather, the ornamental *A. hypochondriacus* of English gardens. Markham wrote that in the Himalaya it was "extensively grown throughout the hills as a staple grain and the bread made from its seeds is the common food of the people." Farther east, in Uttar Pradesh, the species was collected under the name of *A. anardana* by Madden (Appendix). He listed it (1848, p. 443) among the common grain crops of Kumaon, where it was called *chooa* or *ramdana*. On the border between Uttar Pradesh and Nepal, Henry Strachey (1848, p. 109) found the Bhotiya people of the Kali Valley growing crops of red and white amaranths; *A. hypochondriacus* was collected nearby, without comment, by his brother and other contemporaries (Appendix).

Through most of its Asiatic range, the species has been cultivated only on a very small scale, scattered through other crops, in rows along field edges, or in gardens by houses. It has been noted as a staple crop only in the Himalaya and the hills of southern India. Mostly it is planted above 1500 m elevation, continuing nearly to the upper limits of agriculture.

As in Mexico, the crop is ordinarily pale seeded where carefully maintained, but dark seeded plants are often present as scattered individuals and may become predominant where the crop is planted in a desultory fashion or allowed to seed itself. Dark seeded specimens without definite notation of grain use are omitted from the maps because they may be weedy volunteers. For example, collections of millet grain from Karakoram (*Nakao 1157, 1159, 1178*) contained dark amaranth seeds as a contaminant; when grown out (*Sauer* 2534, 2536, 2537, WIS), these proved to be *A. hypochondriacus*. Unfortunately, some grain crop specimens are probably thus excluded. In Iran and Afghanistan in the late 19th century, an unidentified amaranth was reported as a very minor grain crop; the only available *A. hypochondriacus* specimens from this region are dark seeded (e.g. *Johnston s.n.*, 1880, nr Shaikhabad, Afghanistan, E; *Koelz s.n.*, 1940, Saidabad, Kerman, Iran, *kharus*—progeny: *Cowgill* 2354, GH). These lack data on use but the Tajic name on the Koelz specimen is like that reported for the grain crop.

The grain is used in Asia much as it is in Mexico; it is parched and milled, the dough patted into thin tortilla-like pancakes called *chapatis*; it is cooked for gruel; it is popped and made into confections with honey or syrup binder. It is also used in peculiarly Asiatic recipes and there is one fascinating account from India of fermenting the grain for beer (Hunziker, 1952, p. 77). Among Hindus, popped amaranth grain soaked in milk is the only food permitted on certain festival days (Singh, 1961, p. 4), which may simply mean that it entered the scene too recently to be covered by traditional taboos.

At present, the crop seems to be spreading out of the back country into the plains of India. It has recently been reported for the first time around Delhi and in the states of Madhya Pradesh and Gujarat (Singh, 1961, pp. 2-4, 8). The common

name in these regions, *rajgira,* is the same reported for the crop in the Deccan early in the 19th century. Singh states that it is now widely grown in the north Indian plains, usually in scattered patches or mixed with chili peppers, eggplant, and other vegetables; he published a photograph (1961, p. 10) of a mixed crop of *A. hypochondriacus* and eggplant in a Delhi village. In eastern Gujarat near Mehsana and Nadiad, amaranth is grown as a pure crop under intensive cultivation and irrigation, 300 acres yielding about 250,000 lbs of grain, which is mainly shipped to Delhi and other big cities of northern India. Much of it is popped for *laddoos,* confections like the *alegrias* of Mexico, which are sold in the Delhi area by a large number of refugee families from West Pakistan as their sole means of livelihood (Singh, 1961, pp. 4, 20). Another area of important recent cultivation is around Fyzabad in the Gogra plains of Uttar Pradesh; there the pale seeds are called *ramdana,* as they were in parts of the Himalaya over a hundred years ago; they are popped to make confections, especially for the September festival of Janam-Ashtami (Panje, 1960, personal communication). The species has also appeared recently in Maharashtra (Appendix), where it is grown along the edges of fields and in small plots near houses; the grain is cooked with milk and sugar (Kelly, 1960, personal communication).

Other recent records show persistence of the species in areas where it was previously reported. In the south Indian hills, it is still grown under the Tamil name *keerai* reported 150 years ago. Singh (1961, p. 10) published a photograph of *A. hypochondriacus* cultivated by the Badagas of the Nilgiri Hills. In 1962, Noble found a few amaranths grown with maize, beans, and squash near almost every Badaga house (Noble, 1962-64, personal communication). He noted that the Badagas mix stone-ground amaranth meal with sweetened milk to make porridge and pop the grain in a shallow iron pan or in an earthenware pot with a hole in the side. The popped grain is eaten plain or in balls made with honey or syrup. Baskets of it and of other popped cereals are placed as offerings on Badaga funeral pyres. Noble also found the species sown on field edges and scattered through millet fields of the Irula and Kurumba tribes in the Nilgiri Hills and among the Maddi and Chettiar tribes in the Pulni Hills (Appendix). Dark seeded forms of *A. hypochondriacus* are evidently grown in the south Indian hills only as potherbs.

There are many new records of the crop in its old Himalayan regions. In Kashmir, Polunin collected it at several places in 1956, mainly from small plantings on verges of maize fields (Appendix). His notes agree with a statement by Randhawa & Nath (1959-61, **1:** 218) that in Kashmir the grain, called *ganhar, is* parched, ground, and eaten with milk or water, especially by Hindus on fast days. Polunin collected random samples of 25 plants from each of five different localities; three of these included two or three dark seeded plants and the other two lots were entirely dark seeded. In the Karakoram of Gilgit, Nakao (1956, personal communication) met with the species many times, not in fields but in small garden patches; the grain is eaten by the Hunza. Also in Gilgit, Harlan found the species grown for grain in a Shimal garden in 1960 (Appendix).

In northwest India, the crop is still important in the hills and Himalayan valleys of Himachal Pradesh, the Punjab, and Uttar Pradesh. In the Kullu Valley, Punjab, about 2,000 acres yielding perhaps 400,000 lbs of grain were grown in 1956-57; the boiled grain makes a gruel called *phambra* (Singh, 1961, pp. 4, 20). Singh published a striking color photograph of red and yellow *A. hypochondriacus* in the Kullu Valley. In Uttar Pradesh, particularly around Mussoorie, around Tehri in the Kumaon Hills, and all over Garhwal, the grain is milled for bread and thin *chapati* pancakes; confections of popped grain are sold in local bazaars (Singh, 1961, p. 4; Lal, 1961, personal communication; Andress, 1965, personal communication). Andress found *A. hypochondriacus,* called *chaulai,* one of the staple monsoon crops in the mountains around Mussoorie; it is planted alone or with millets, often on very poor, stony ground; at elevations above 1800 m it yields better than almost any other crop but is considered inferior in taste to true cereals. The 1952 Oxford University Expedition to Tehri-Garhwal found fields of the crop reddening the landscape around Harsil, a village at 2500 m elevation in the Bhagirathi Valley. Harsil is occupied seasonally by Hindu farmers and Bhotiya-related traders who are intermediaries between the Hindus and Tibetans. Photographs of the crop at Harsil (Fig. 6-7) were taken by Tyson, the expedition leader; one has previously been published in color (Tyson, 1953, p. 140). Specimens were collected (Appendix) by an expedition member, Paul Huggins, who died a few days later on a descent from Gangotri peak.

In western Nepal in 1953, Tyson found the species at Biunera, an unmapped village 25 miles due east of Baitadi, and also at Chainpur, 20 miles farther east in the Seti Valley; at both places the crop is called *marcha* and flour made from the grain is called *ata* (Appendix; Tyson, 1954, personal communication). Hagen (1960, p. 388) published a fine color photograph of a field of *A. hypochondriacus* in the Kuwari Valley of western Nepal, where the grain is popped and ground for flour. In central Nepal in 1952-53, the Japanese Himalayan Expedition found little patches of grain amaranths were a characteristic feature of the agricultural landscape, especially on newly cleared mountain slopes. The mixed red and yellow spikes were very colorful when the crop was maturing in the fall. Photographs taken on this expedition by Nakao show *A. hypochondriacus* as an aftercrop in a maize field near Jagat in the Marsyandi Valley, about 20 miles southeast of Annapurna (Nakao, 1956, p. 101, *plate 14;* Nakao & Sauer, 1956, p. 143). Nakao also collected the crop 40 miles farther east at Tsumje and Thomje in the Shiar Kola Valley (Appendix). It is generally called *nana* by the Nepalese, *pilim* by the Sherpa; the grain is boiled for gruel and ground for flour.

I have no new information on the species in China except from Manchuria. In 1956, Hanelt saw small plots of grain amaranths there, particularly near Harbin and Chiamussu in Heilunkiang; they were cultivated at the margins of fields of farmers and cooperatives (Hanelt, 1958, personal communication). Hanelt also obtained a specimen from an agricultural experiment station in Kirin (Appendix). Nakao (1957, p. 409) saw a field of *A. hypochondriacus* in the Kirin area in 1944.

A surprising outpost of *A. hypochondriacus* appeared recently in Uganda, where it was collected in 1945 and 1946 as a grain crop in the Masaka District

Fig. 6. Walled field of *A. hypochondriacus,* Harsil, Tehir-Garhwal, India. [Photo J. Tyson]

Fig. 7. Patch of mature *A. hypochondriacus* in garden, Harsil, Tehri-Garhwal, India. [Photo J. Tyson]

(Appendix). According to Purseglove (1964, personal communication), during World War II, when imported Indian food grains, mainly pulses and amaranth, became increasingly scarce in east Africa, the local Indian population provided seed for planting by African cultivators. The first small amaranth crop was sold in 1943 at a shilling per lb. By 1945, 66 tons of the grain were sold in Masaka at a much lower price. The grain was used primarily on Hindu fast days and was not known to have been eaten by Africans.

Amaranthus hypochondriacus as a Cosmopolitan Ornamental.

There is no record that the American Indians ever planted this species primarily for its color or as a dye plant, but they evidently favor red and yellow forms in the grain crop. Such pigmentation was the main reason the species was taken into European gardens. Selected forms, scarcely gaudier than those of the aboriginal grain crop, have been widely disseminated as ornamentals, particularly in temperate regions with a European gardening tradition. These ornamentals are invariably dark seeded, as are all specimens of *A. hypochondriacus* known from European botanical gardens, even those from the 18th century.

It is uncertain how long the species had been in Europe before Linnaeus encountered it in Clifford's garden in Holland early in the 18th century. It may be represented in some puzzling earlier descriptions of amaranths grown in European gardens, some dating back to the 16th century, but it is possible that all of these were forms of *A. caudatus*. Older common names for ornamental amaranths in Europe, such as flower-gentle, *floramour* and *Mayer*, were highly ambiguous and even shared with ornamentals in other genera, *Celosia* and *Gomphrena*. The distinctive English name for *A. hypochondriacus*, Prince-of-Wales'-feather or prince's-feather, appeared in the early 19th century.

Amaranthus cruentus L., Syst. Nat. ed. 10. **2:** 1269, 1759.

The phrase-name, *A. racemis pentandris compositis patulo-nutantibus, fol. lanceolata-ovatis*, is appropriate but inadequate for identification. In the 1763 edition of the Species Plantarum, Linnaeus inserted China as the habitat and cited *A. sinensis foliis variis* Mart. (Martyn, 1728-37, *pl.* 6) as a synonym. Martyn's plate, a fair likeness of the species, was drawn from "Chinese" plants cultivated in gardens around London. There is a specimen in the Linnaean herbarium labelled *A. cruentus* (LINN 1117.25).

A. paniculatus L., Sp. Pl. ed. 2, **2:** 1406, 1763.

The phrase-name, *A. racemis pentandris supradecompositis, partialibus patentibus*, is compatible with but not diagnostic of the species. Linnaeus noted that *A. paniculatus* resembled *A. cruentus*, but was taller, and gave the habitat as America. There is a specimen in the Linnaean herbarium labelled *A. paniculatus* (LINN 1117.20).

A. sanguineus L., Sp. Pl. ed. 2, **2:** 1407, 1763 (pro parte).

Linnaeus' description is ambiguous. He cited a description and plate of a plant grown by Miller from Bahamas seed; I have seen only a later reproduction (Miller, 1768), which is evidently *A. cruentus*. A specimen in the Linnaean herbarium labelled *A. sanguineus* (LINN 1117.21) belongs to *A. caudatus*.

A. speciosus Sims, Curtis Bot. Mag. **48:** 2227, 1821.

The plate, which is a fair likeness of *A. cruentus,* is based on plants grown in England in the garden of Sir George Staunton, Leigh Park, from Nepal seeds obtained from H. I. Colebrook. There is no doubt that *A. cruentus* was in Nepal at the time; specimens collected there by N. Wallich in 1821, labelled *A. speciosus,* are in the Moquin-Tandon herbarium (P) and the de Candolle herbarium (G).

Amaranthus cruentus evidently originated as a domesticated grain crop somewhere in southern Mexico or Guatemala, the only region where it is found in aboriginal cultivation within the range of its probable progenitor, *A. hybridus.* Its wide range as a dye plant, ornamental, and potherb is certainly secondary, although not necessarily entirely modern.

As a rule, the species is extraordinarily homogenous but there is some diversity in pigmentation within the grain area and some other local variation attributable to hybridization with other species. The *A. cruentus* grain crop is often intimately associated with weedy populations of its probable progenitor, *A. hybridus,* and it is easy to find traces of introgression on both sides. However, interbreeding has evidently been limited by natural selection against hybrids in the weed populations and artificial elimination of hybrids, especially those with dark seeds, from the crop. Crossing with the other North American grain crop, *A. hypochondriacus,* has more pervasive effects; the few collections of *A. cruentus* as a Mexican grain crop all show definite traces of such crossing (Appendix). Where *A. cruentus* is grown as a Pueblo dye plant within the native range of *A. powellii,* hybridization with the latter occurs (Bohrer, 1960, p. 199). As a cosmopolitan ornamental, *A. cruentus* has occasionally mixed with weedy populations of *A. powellii, A. hybridus,* and *A. retroflexus.* The resulting hybrids are partly sterile and usually ephemeral, but some have developed into locally successful weeds (Tucker and Sauer, 1958, p. 260; Grant, 1959b, p. 320).

Amaranthus cruentus as a New World Grain Crop (Fig. 1).

The species has not been identified archaeologically. It is, of course, not certain that the *zoale* paste found in the prehistoric Mixtec tomb at Monte Alban was made from *A. hypochondriacus* grain, as suggested above, rather than from *A. cruentus.* The former species is more important in Oaxaca today, but Kaplan recently collected *A. cruentus* among the Mixtec near the Pacific coast (Appendix). Called *chian,* which ordinarily refers to *Salvia,* it is grown only by the Indians, who sow it as a minor crop in milpas with maize or by itself; the milled grain is used for *atole* and mixed with maize for tortillas (Kaplan, 1954, personal communication). The few previous records of the species from Mexico (Appendix) suggest it was locally a minor component of the grain amaranth crop, indistinguishable in historical records from the dominant *A. hypochondriacus.*

In Guatemala the situation was reversed, *A. cruentus* being the more important of the two, although it is now a declining relic. In 1947, it was regularly grown in a few temperate zone villages in the departments of Guatemala and Chimaltenango and in a lower-lying region in Alta Verapaz, usually on a very small scale. Both pale and dark seeded forms were present; both were called *bledo* in Spanish

Fig. 8. Semi-cultivated plant of *A. cruentus*, edge of milpa, nr San Juan Sacatepequez, Guatemala. [Photo J. D. Sauer]

and variants of *tez* in the Maya dialects. Dark seed was used only for tortillas; the pale seed was much preferred for tortillas and was prepared in various other ways, much like maize, for home consumption. It was also popped for confections identical to the *alegrias* of Mexico, but here called *niguas*, which were peddled widely at certain seasons.

Revisiting some of these areas in 1966, I could find only vestiges of the crop. Between San Juan Sacatepequez and San Raimundo in the department of Guatemala and near El Tejar in Chimaltenango, plants of *A. cruentus* are still conspicuous along the edges of some milpas and in a few dooryard gardens (Fig. 8). However, all the plants seen were said to be volunteers or planted simply by scattering some seed at the time of harvest. Moreover, all the plants were dark seeded and I could find nobody that had a supply of the pale seed. The farmers all knew about *niguas* but said they were now not often made, being more expensive than a similar confection, *alborotos*, made of popped sorghum grain.

I have not been back to Alta Verapaz to see whether the crop persists there, but in 1965 small scale cultivation was encountered not far away by Barbara Denton and Alan Covich; they found *A. cruentus* grown, under the name *ses*, at Ensenada and El Estor in the lowlands of Izabal, the grain being milled and made into little cakes as confections (Covich, 1966, personal communication).

Amaranthus cruentus as a New World Dye and Ceremonial Plant.

The domesticators of the species may have been at least incidentally interested in coloration of the plants from the start and forms evidently selected for striking

pigmentation were carried in the Central American grain crop. However, the only American Indian peoples known to have planted the species primarily for its pigment were the Pueblos of the Southwest. A special form with the whole plant body as red as a beet was grown by the Hopi, Zuñi, and Rio Grande pueblos. A water extract of the entire inflorescence was used to dye the pink maize wafer bread for ceremonial dances. The seeds, invariably dark, were apparently not eaten. The Hopi had their own name, *komo,* for this plant but the Mexican name *alegria* was used in the eastern pueblos. The only hints of a possible aboriginal track northward from Central America are an old collection of *A. cruentus* grown for unknown reasons in the Tarahumar area of Chihuahua and a report of an unidentified bright red amaranth used to color maize dough in Guerrero (Sauer, 1950b, pp. 412-414).

During the 19th century, the Pueblo dye amaranth was carefully cultivated in irrigated terrace gardens but the Hopi have lately neglected it, substituting vegetable coloring bought from the trader (Farmer, 1953, personal communication). In Zuñi gardens it is now mostly allowed to reseed itself and it is gradually being lost by crossing with the weedy *A. powellii* (Bohrer, 1960, p. 199).

Amaranthus cruentus as a Cosmopolitan Ornamental and Potherb.

Dark seeded forms of the species, some approaching the Pueblo dye form in intensity of plant color, are now commonly grown in the wet tropics and some temperate regions. Ordinarily they are planted in gardens as ornamentals and potherbs; occasionally they have magical, imaginary medicinal, or other esoteric functions.

The present range of planting as an ornamental and potherb includes the grain crop region; in fact, *A. cruentus* is the commonest garden amaranth of Central America in general. How much of this range was aboriginal is unknown. By the time the species distribution began to be revealed by extensive botanical collecting, it had already been adopted into non-indigenous cultivation throughout Latin America and far beyond.

As noted in the discussion of nomenclature, the species reached Europe in the early and mid 18th century via China, the Bahamas, and other unspecified New World sources. The original European descriptions show that bright red or deep red forms were introduced at the start. Martyn (1728-37) praised it as elegant and colorful. Miller (1768) said the plants were beautiful and gay the first two years they were sown in England but afterward the seed degenerated. However, stabilized color forms are still widely grown in European style gardens, often called cockscomb like the distant relative, *Celosia argentea.*

In the Old World tropics, the chronology and geography of the species' immigration are quite mysterious. As already noted, it was attributed to China and India in 18th century literature and collected in Nepal in 1821. By 1850, it was common in south India (e.g. Madras collections by *Buchanan-Hamilton, Elliott, Thomson,* & *Wight,* all E). It is still commonly planted as a potherb there and the seeds are sold in commercial packets. The Badagas, who cultivate *A. hypochondriacus* as a grain crop high in the Nilgiri Hills, plant *A. cruentus* as a potherb

in lower sites (*Noble s.n.*, 1963, Marakari, WIS). Asiatic cultivation of *A. cruentus* is mostly outside the grain amaranth regions, and extends through the tropical and warm temperate parts of India, Indo-China, China, Japan, the Philippines, and Indonesia. In New Guinea, it has been found as a fetish planted among the crops (*Stoner s.n.*, 1949, nr Lae—progeny: *Sauer 1536*, WIS). There are collections from a few Pacific islands, the earliest (1860) from Fiji (*Seemann 367*, GH).

In tropical Africa, *A. cruentus* has had a remarkable distribution as a potherb, ornamental, and for superstitious medicine. It was collected on Livingstone's expeditions in the Zambesi and Nyassa regions in 1859 and 1861, on Speke and Grant's expedition in the Lake Albert and Lake Victoria regions in 1862, by Burton in the Congo in 1863, Schweinfurth on the Sudan-Ethiopian border in 1865, Welwitsch in Angola in 1879 (all K), and by innumerable later explorers from French Guinea through the heart of the continent to the east coast and Zanzibar. The only record suggesting cultivation as a grain crop is a note on one collection that the seeds are edible (*Scott-Elliott 4653*, 1891, Sierra Leone, K). *Amaranthus cruentus* is almost certainly the source of the beloved red dyestuff that Dammer (1895, p. 402) reported was obtained from the large blood red inflorescences of an amaranth much cultivated in the Lake Region of East Africa. Dammer called the species *A. caudatus*, which is actually scarcely known in tropical Africa outside Ethiopia. In African botanical literature and herbarium collections, *A. cruentus* usually masquerades as *A. caudatus*.

Amaranthus caudatus L., Sp. Pl. 990, 1753.

The phrase-name, *A. racemis pentandris cylindricis pendulis longissimis*, which is diagnostic, derives from Linnaeus' Hortus Cliffortianus of 1737. Evidently he first became acquainted with the species in Clifford's garden in Holland, where it was recognized as a South American native. Linnaeus later connected it by citations in his Hortus Zeylanicus of 1747 with Ceylon plants collected by Hermann in the 1670's, and in his Hortus Upsalensis of 1748 with plants grown in Sweden. Other synonyms cited in the Species Plantarum are *A. maximus* Bauh. (Bauhin, 1623, p. 120) and *Blitum majus peruvianum* Clus. (Clusius, 1601, **4:** 81). Linnaeus gave Peru, Persia, and Ceylon as habitats, the first evidently after Clusius, the others after Hermann, who called his Ceylon plants *Blitum persicum maximum*, for reasons unknown. All these cited names probably are actually synonymous, although not all are positively identified. There is a specimen bearing Bauhin's name, *A. maximus*, in the Hortus Cliffortianus herbarium (BM) and a specimen labelled *A. caudatus* from the Uppsala Botanic Garden (LINN 1117.26).

A. sanguineus L., Sp. Pl. ed. 2. **2:** 1407, 1763 (pro parte see synonymy under *A. cruentus*).

A. caudatus L. (var.) *δ alopecurus* Moq.-Tand. in DC., Prodr. **13**(2): 256, 1849.

Type: Ethiopia, nr Aduwa, ruderal, 1 Nov 1844, *Schimper 1535*, Moquin-Tandon herbarium, P; isotypes G, GH, K, MO, US. Another collection was cited from the same locality: 10 Nov 1838, *Schimper 1077*, G, MO, US. (*A. alopecurus* Hochst. ex A. Br. et Bouché, Ind. Sem. Hort. Berol. App. 1, 1872, is based on the same specimens as Moquin-Tandon's variety; in both cases, the name was taken from Hochstetter's nomen nudum on the printed labels of Schimper's collections).

A. mantegazzianus Passerini, Ind. Sem. Hort. Bot. Parma, 4, 1865.

Based on plants grown in Italy; seed obtained by Mantegazza from grain crop, *quinoa blanca,* in Salta and Jujuy, Argentina. Neotype designated by Hunziker (1951, p. 105): Argentina, Colalao del Valle, Tucuman, grain crop, *chaclion, quinoa de Castilla,* 23 Mar 1943, *Hunziker* 2555, CORD (not seen); duplicates K, S, SI, US.

A. edulis Spegazzini, Physis 3: 163, 1917.

Type: Argentina, plants grown at La Plata from seeds of Indian grain crop, *trigo inca,* collected in 1897 at Amblayo, Salta, *Spegazzini, s.n.,* LP 16.325 (not seen, but Hunziker's description of the type (1943, pp. 322-323) is meticulous).

Amaranthus caudatus probably originated by domestication of *A. quitensis* as an ancient Andean grain crop. Its wide introduction elsewhere as a grain crop and ornamental is certainly secondary and probably post-Columbian.

The species, like other grain amaranths, has a spectrum of plant color forms. It also has some variations in inflorescence structure and seed color not found in any other *Amaranthus* species. The *A. caudatus* grain crop includes a variety of inflorescence types, some resembling those of other domesticated amaranths, some with peculiar drooping branches; the commonest ornamental has an almost unbranched, pendulous inflorescence like a long, red tail. An even more bizarre form has inflorescence branches with determinate growth, each tipped by an abnormal polymerous staminate flower; as a result, the inflorescence branches become club shaped rather than tapering toward a continuously growing tip. This form is known only from northwest Argentina, where it is planted as a grain alone or together with ordinary *A. caudatus.* It has been given species rank, as *A. edulis* or *A. mantegazzianus,* but is probably merely a conspicuous mutant. No possible progenitor other than *A. caudatus* is known.

Some forms of *A. caudatus* have ordinary wild type dark seeds or plain ivory seeds like the other grain species, but the commonest forms have ivory seeds flushed with red around the rim. Unfortunately, this unique character of *A. caudatus* usually cannot be detected on older specimens because the red tinge fades.

In its native area, the species has some variation attributable to local interbreeding with weedy populations of *A. quitensis.* In its wide migrations as a crop and ornamental, *A. caudatus* has repeatedly mixed with various weed relatives and may have contributed to some complex hybrid weed populations (Tucker and Sauer, 1958, p. 260). However, most forms of *A. caudatus* show no trace of hybridization with weeds or other domesticates. Even in Asia, where *A. caudatus* and *A. hypochondriacus* now share an enormous range as grain crops, only a few sterile hybrids are known (e.g. *Hooker s.n.,* Sikkim, L).

Amaranthus caudatus as a New World Grain Crop (Fig. 9).

The oldest record of the species is from an urn found in a late pre-historic site in Salta, Argentina; it contained flowers and both pale and dark seeds of *A. caudatus,* together with maize, beans, and chenopod seeds. The crop is not usually distinguishable in early chronicles from the superficially similar *Chenopodium quinoa;* both often share the common name *quinoa* and are grown as grain crops by the same Andean peoples. Hunziker (1952, p. 74) points out that *A. caudatus*

had an advantage over *Chenopodium* in mountainous regions where water was scarce, because its grain is free from the bitter saponins that must be leached out of chenopod grain.

The first recognizable reference to *A. caudatus* as a grain crop was the description and illustration of *Quinua sive Blitum majus peruvianum* by Clusius (1601). In 1635 in Ayacucho, Peru, red and white amaranths were very common foods of the Indians, and the seeds of the white form were also made into confections.

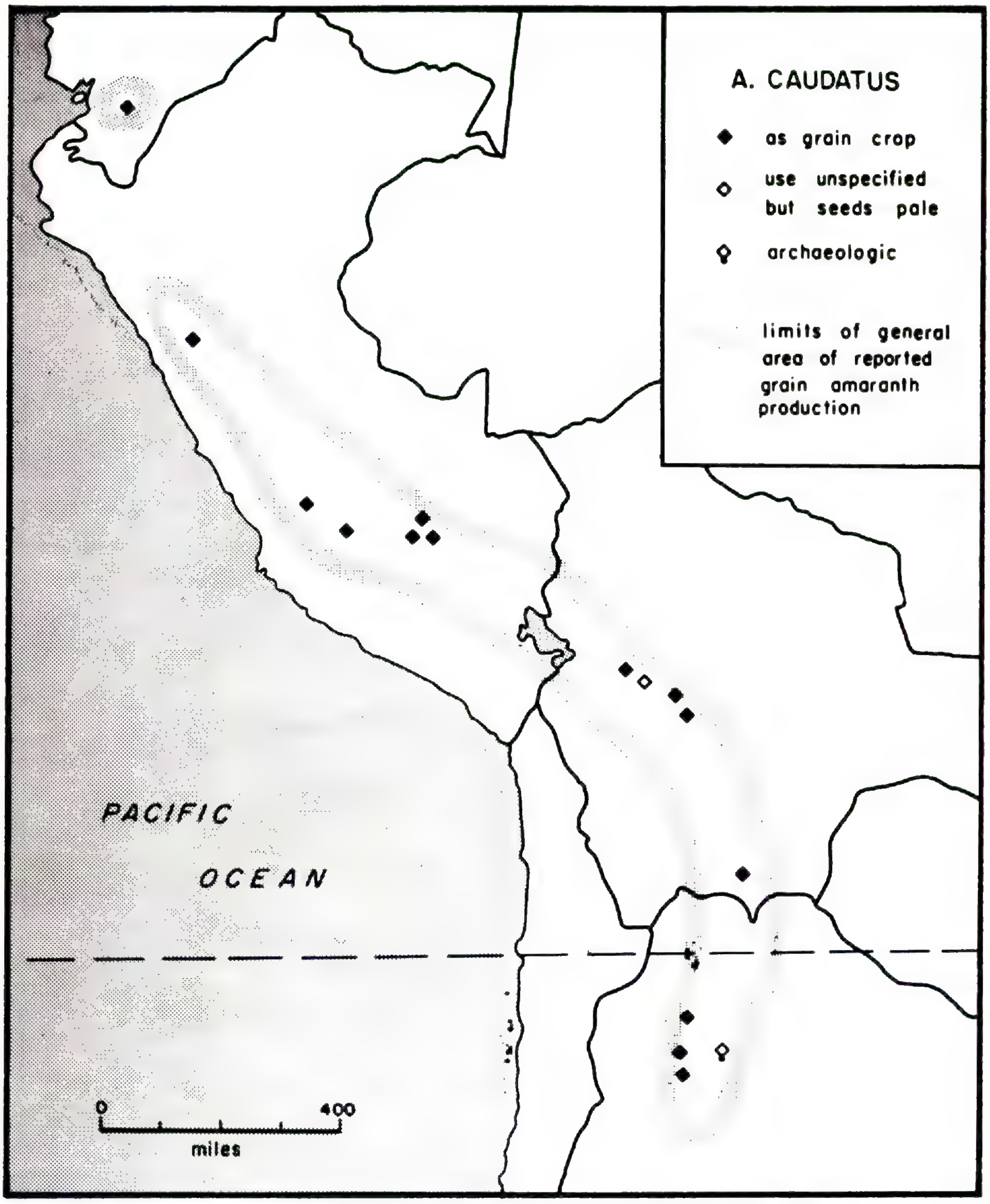

Fig. 9. South American distribution of grain amaranths.

Modern botanical exploration, beginning late in the 19th century, has turned up many cases of cultivation in temperate and cool temperate valleys of Peru, Bolivia, and Argentina. The crop is grown only by Indian peoples, usually in very small plantings near houses or on the edges of maize fields. The grain is toasted and popped, boiled for gruel or stews, or ground into flour. Pale seeds, reddish tinged or plain, are preferred but some dark seeds are often mixed in the harvested grain.

The crop is obviously a declining relic and there are few new records. In Bolivia, Urquidi (1954, p. 151) and Henkel (1966, personal communication) report persistent cultivation in the department of Cochabamba; a row of plants is grown along the edges of maize fields, the toasted grain being used especially for children or invalids and the stalks being useful in fencing and roof construction. There are recent collections of the species as a minor grain from several places in Bolivia and Peru (Appendix). Commerce in the grain in the Cuzco region has been described (Hunziker, 1952, pp. 74-75) as conducted by witch-doctors from the Altiplano; they carry bags of amaranth flour for sale to the natives, who mix it into *chicha* and consider it excellent food.

In Ecuador, the first known record of the crop was a note by Luis Cordero in 1950 (cited by Heiser, 1964, p. 137) that the grain of an amaranth called *quinua de tostar* was eaten in the provinces of Azuay and Cañar. In 1966, Heiser found several Indian families in this region cultivating *A. caudatus* for grain under the name *quinoa* (Appendix; Heiser, 1966, personal communication).

Amaranthus caudatus as an Old World Grain Crop (Fig. 4-5).

The species had been introduced to Asia before 1700, if Linnaeus identified Hermann's Ceylon plants correctly. The oldest available Asiatic specimens were collected in northern India and Nepal in the early 19th century. By the middle of the century it had been found scattered widely through the Himalaya and into Afghanistan; before 1900 it was in China as far north as Manchuria (Appendix). The listed specimens have pale, sometimes reddish, seeds; dark seeded forms were also collected early but more rarely in Asia (e.g. *A. von Schlagintweit 5720*, 1856, Baltistan, E; *H. & R. von Schlagintweit 1482*, 1856, Ladak, GH).

None of the early collections bear data on purpose of cultivation, but in the present century pale seeded forms have been recorded as a grain crop at several places in the Himalaya and China. Uses are similar to *A. hypochondriacus*, which is grown at more places and in larger quantities over the same general range.

There are some additional records from Asia. The Japanese Expedition to Nepal Himalaya found *A. caudatus* grown for grain at three villages on the slopes of Annapurna in 1953 (Appendix; Nakao & Sauer, 1956, p. 142). It was recently photographed growing with millet in the Kullu Valley, Punjab; there and in India in general, it is grown only as scattered plants or in very small plots and is less common and important than *A. hypochondriacus* (Singh, 1961, pp. 12-14). In the Nilgiri Hills of Madras, the Kurumbas, who commonly cultivate *A. hypochondriacus*, occasionally also plant *A. caudatus* for grain and as a potherb (Appendix; Noble, 1963, personal communication). Nearby in the Pulni Hills, Noble

obtained a lot of amaranth seeds intended for popping; when grown out, they proved to be a mixture of *A. hypochondriacus* and *A. caudatus* (Appendix). In Suiyan province, Inner Mongolia, a field planted to *A. caudatus* was seen in 1944 (Nakao, 1957, p. 409).

The only other area where the species is known in folk cultivation is Ethiopia. The older specimens are all dark seeded and are not known to represent a regular grain crop. The earliest known collection (*Pearce s.n.*, ca 1815, Tigre, BM) was said by Pearce to be the most beautiful flower he had seen in Abyssinia. He noted that the Abyssinians parched the seeds and ate them for complaints in the stomach and breast; the name was *Tsellal Enno Mariamm* (parasol of the Virgin Mary). This name was reported for other specimens from Tigre (*Schimper 359, 1077, 1513, 1535*, 1837-44, nr Aduwa, BM, G, GH, K, MO, P, US). There have been later collections of the same dark seeded form from Ethiopia (e.g. *Cooper s.n.*, 1926 Addis Alam, Shoa Prov, K) and from the Sudan (*Lynes 596*, 1921, Darfur Prov, US), but none have data on use. Finally, near Jimma in 1957, Anderson found that *A. caudatus* grain is eaten popped and milled and the inflorescences are used to decorate the cross for Mascal Day processions; forms with both dark and pale, reddish tinged seeds were collected (Anderson, 1957, personal communication; Appendix). The plants are allowed to seed themselves and also sown along field edges and in rubbish heaps by houses. The seed was said to have been brought originally from the Maji forest region, where the Ghimera regularly cultivate it as an important grain. Meyer subsequently collected pale, reddish tinged seeds of *A. caudatus* in the forest districts of southwestern Ethiopia, where it is a grain of Negro tribesmen (Appendix).

Amaranthus caudatus as a Cosmopolitan Ornamental.

It is certain that some pale seeded American grain amaranths had been introduced to European gardens during the 16th century (Gesner, 1561, p. 246; Gerarde, 1597, p. 254,) and were soon widely grown as ornamentals and for medicinal uses inspired by their blood red color. It is possible that *A. caudatus* was the only American amaranth planted in Europe during the 16th and 17th centuries, but this is not certain. The distinctive form of *A. caudatus* that was to become the common ornamental was first clearly described by Parkinson (1640, p. 753) and Ray (1686-88, **1:** 202). This has since gone around the world, often in commercial seed packets, and is still widely planted, especially in temperate zone gardens. Its peculiar English name, love-lies-bleeding, seems to be a Victorian invention. In other languages it shares names such as red-hot-cattail, fox-tail, or scourge-of-the-nun with the unrelated but curiously similar chenille plant, *Acalypha hispida*.

Discussion and Conclusions

Amaranth domestication may have begun, as has been repeatedly suggested, with the very beginnings of American Indian agriculture. Some arguments for early domestication, such as the central role of the crop in pre-Conquest Mexican ceremonials, are fairly convincing but they are not based on direct evidence. So

far, archaeologic amaranth seeds that are known to be very ancient may have been merely gathered. In both North and South America, finds of definitely domesticated grain go back only to late prehistoric times.

It has been more or less taken for granted that each grain species was separately domesticated in a particular region and period, then carried into other regions and passed down through time like a uniquely invented culture trait. Some alternative possibilities have not been ruled out, one being multiple domestications of the same wild species. The progenitors of the grain amaranths would seem to be ideal candidates for repeated domestication, being naturally wide ranging, weedy, and obviously useful plants. However, what little variation there is within the domesticated species does not suggest an old heritage from distinct geographic races so much as it does recent introgression.

Another conceivable possibility is derivation of two or even all three grain species from a single primary domesticate. For example, *A. cruentus* might have been domesticated from *A. hybridus* in humid regions of Central America and then carried northwestward into drier highlands, where it picked up *A. powellii* as a weed. By continued crossing with *A. powellii,* the Mexican grain crop might eventually have come to resemble it more than its original progenitor. Similarly, southward carriage of *A. cruentus* followed by repeated crossing with *A. quitensis* might have produced the distinctive Andean grain crop, assuming that *A. cruentus* and *A. quitensis* can interbreed, which is not proven.

The main reason for considering such a speculative connection between domesticated species is that it would account very simply for some peculiar characters shared by all three. Of these, the pale seed character seems hardest to explain by convergent evolution in three independent evolutionary lines. Mutants producing pale seeds have never been recorded in any wild amaranth species nor in the dark seeded ornamental forms of the grain species. It would be worth knowing whether the pale seed character is genetically homologous in the domesticated species, but this has not been investigated.

Thus, although alternatives should be kept open, it is still possible to maintain the simplest, most obvious hypothesis, namely that the three grain species were independently domesticated by different prehistoric peoples of North and South America.

As for the intriguing problem of when and how the species were introduced to the Old World, the evidence remains inconclusive. There is no proof that any of them were in the Old World before Columbus. On the other hand, their spread in Asiatic and African cultivation certainly outran European contacts and could scarcely have been initiated by any direct transfer between Old and New World colonies of the same European power. Introduction through Europe itself seems most likely in the case of the Andean *A. caudatus.* Pale seeded forms evidently were taken there directly from South America in the 16th century, long before they were found in Asia or Africa. However, dark seeded forms that are minor components of the Andean crop somehow became established in remote parts of Asia and Africa before they were known in Europe.

The Mexican *A. hypochondriacus* and the Central American *A. cruentus* evi-

dently reached Europe in the 18th century, both arriving via Asia and directly from America. Europe got only dark seeded forms that are inferior as grain and grown mainly as potherbs and ornamentals. The pale seeded forms of *A. cruentus* apparently never left Central America but pale seeded *A. hypochondriacus* had reached Asia by the 18th century. At least since the early 19th century, *A. hypochondriacus* has been a widespread and locally important grain crop there. At present, India alone undoubtedly harvests more grain from this one species than is produced by all the relics of grain amaranth cultivation in the New World.

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Appendix: Grain Amaranth Specimens Examined

Specimens cited are either reported as grown for grain or are pale seeded forms from known grain amaranth regions. (The only other pale seeded specimens belong to the common ornamental race of *A. caudatus*.) Collections of the author are indicated by J.D.S.

Notations between hyphens:

-G: grain use specified
-N: grain use not noted
d-: seeds dark
p-: seeds pale
i-: seeds immature
@: strongly atypical, apparently hybrid

Amaranthus hypochondriacus

America. guatemala. alta verapaz: *Pittier 197* (in 1905), nr Secanquim -Np- (US).

Mexico. chihuahua: *Gentry 1843, 1844* (in 1935), Warihio Indian village, Guasaremos, *guegui* -Gp- (MO, UC, US); *Gentry s.n.* (in 1948), seed from Rancho Trigo, Sierra Chamco, *bledo* or *guegui*—progeny: *J.D.S. 1193* -Gp- @ (MO, WIS). *Pennington 269* (in 1960), Tepehuan settlement nr Santa Rosa, *giage* or *guatle* -Np- (WIS). distrito federal: *Martinez s.n.* (in 1917), *alegria* -Gp- (US). *Bravo s.n.* (in 1940), seed from Valley of Mexico, *alegria*—progeny: *Hunziker 2948* -GP- (GH). *Kelly s.n.* (in 1947), betw Xochimilco & Tlahuac -Gp- (UC). *J.D.S. 1171* (in 1947), San Gregorio Atlapulco, *alegria* -Gp- (F, GH, MO, UC, US, WIS). guerrero: *Hernandez X. 3166* (in 1947), seed from Chilapa, *alegria*—progeny: *J.D.S. 1162* -Gp- (F, GH, MO, UC, US, WIS). jalisco: *Palmer 694, 695* (in 1886), Guadalajara, *alegria* -Gp- (K, MICH, US). *J.D.S. 1174* (in 1947), Tlajomulco, *alegria* or *zoale* -Gpd- (F, GH, MO, UC, US, WIS). mexico: *Hinton 2137* (in 1932), Temascaltepec, *alegria* -Np- (K, MO, US). michoacan: *West s.n.* (in 1946), seed from Teremendo, Zacapu *pati* or *alegria blanca*—progeny: *J.D.S. 1170* -Gp- (DS, MO, UC, US, WIS); *West s.n.*, seed from Opopeo, *alegria blanca*—progeny: *J.D.S. 1274* -Gp- (WIS); *West s.n.*, seed from Los Reyes highlands, Pomatacuaro, *alegria negra*—progeny: *J.D.S. 1355* -Gd- @ (MO, WIS). oaxaca: *C. O. Sauer s.n.* (in 1945), seed from Zapotec village of San Juan nr Ixtlan de Juarez, *alegria*—progeny: *Reed s.n.* -Gp- @ (UC) and *J.D.S. 1161* -Gpd- @ (MO, TENN, WIS). *J.D.S. 1266* (in 1947), Clavillones in Zimatlan area, *alegria* -Gp @ (MO, WIS). puebla: *C. O. Sauer s.n.* (in 1948), seed from San Jeronimo Teocuizmanalco nr Tezmelucan, *alegria*—progeny: *J.D.S. 1239* -Gp- (WIS). sinaloa: *Gentry 6547* (in 1941), Quebrada de Manzana, Sierra Surotato, *bledo* -Gi- (MO). tlaxcala: *J.D.S. 1173, 1277* (in 1947), San Miguel del Milagro, *alegria* -Gp- (DAV, F, GAT, GH, MO, UC, US, WIS). *Hernandez X. 3715* (in 1948), seed from San Bernabé Amaxac, alegria—progeny: *J.D.S. 1535* -Gp- (F, GH, MO, UC, US, WIS).

United States. Arizona: (Archaeologic specimens noted in text.) *Powell s.n.* (ca 1870), seed from Arizona Indians—progeny grown at Harvard Univ -Gp- (GH, MO, US).

Asia. Bhutan. *Cooper 2759* (in 1914), Punakha -Np- (E); *Cooper 2501, 3363*, s. loc. -Np- (E).

Ceylon. *Koenig 29* (ca 1780), s. loc., *ette tampala* -Gp- (L). *Macrae 837* (ca 1830), s. loc. -Np- (BM). *Brodie 101* (ca 1850), *101* s. loc. -Np- (E). *Thwaites s.n.* (in 1860), Tricomalee -Np- (K). *Deschamps s.n.* (in 1890), Teldeniya, *rana tampala* -Np- (G).

CHINA. HEILUNGKIANG: *Dorsett & Dorsett 4089* (in 1925), Hsiaoling -Np- (UC, US). HOPEH: *Beach s.n.* (in 1948), Hsin Chi -Gp- (UC). HUPEH: *Henry 2390* (ca 1885), Patung dist, *jua-ku* -Np- (K); *2732*, Ichang, *jua-ku* -Np- (BM, K, US); *Henry 4808*, s. loc. -Np- (GH). *Chow 1294* (in 1934), *Chienshih* -Np- (E). KIREN: *Hanelt 6014* (in 1958), experiment station, Tung Hua -Gp- (GAT, WIS). KWEICHOW: *Tsiang 5946* (in 1930), Yunfoushan, Tuyan -Np- (K). *Steward et al. 784* (in 1931), Fan Ching Shan, Ta Ho Yen -Npd- (GH, K, L, US). SHENSI: *Rev. Fr. Hugh s.n.* (about 1900), Isay Toe, Pao Chi -Np- (BM). SZECHWAN: *Hosie s.n.* (in 1904), betw Batang & Tachienlu -Np- (K). *Yü 14480* (in 1937), Muli, Wachin, Shawan -Np- (E). *Chang s.n.* (in 1948), seed from Muping—progeny: *J.D.S. 1489* -Gp- (F, GH, MO, UC, US, WIS); *Chang s.n.*, seed from Mowhsien—progeny: *J.D.S. 1484, 1499* -Gpd- (DAV, F, GH, MO, UC, US, WIS). YUNNAN: *Ward 3522* (in 1919), Imaw Bum to Hpimaw, *yü-mi* -Gp- (E).

INDIA. Without province: *Roxburgh s.n.* (ca 1800), -Gp- (K). *Wallich 238* (in 1815), -Gp- (BM). *Royle s.n.* (about 1830), NW India -Np- (K). *Ritchie 631* (ca 1840), -Np- (E, GH). *Simpson s.n.* (ca 1840), *Himalaya* -Np- (G). *Wight s.n.* (ca 1840), -Np- (UC, W). *Edgeworth s.n.* (in 1844), NW India, *batou* -Gp- (K). *Falconer 823* (ca 1850), -Np- (K). *Gamble 2028A* (in 1876), -Np- (K). BIHAR: *Buchanan-Hamilton 2028-1* (in 1813), (*Wallich 6903*), Bhagalpur -Gp- (E, P). HIMACHAL PRADESH: *Lady Dalhousie s.n.* (in 1831), Simla -Np- (E). *Thomson s.n.* (in 1847), Serahan, Sutlej Valley -Gp- (K). *Grant s.n.* (about 1850), Kunamer, Sutlej Valley -Np- (K). *Drummond 26070* (in 1886), Simla Hills -Np- (K). *Lace 1483* (in 1896), Chamba -Np- (E). *Harsukh s.n.* (in 1899), Pangi, Sauch Valley, Chamba -Np- (K). *Koelz 7279* (in 1933), Li, Bashahr -Gd- (G, US). MADRAS: *Wight s.n.* (ca 1850), s. loc. -Np- (E); *Wight 1787*, Dindigul Hills -Np- (E); *Wight 2436*, Koathagerry -Np- (K). *Cleghorn s.n.* (in 1859), Kalhatti -Np- (E). *Barber 8603*, (in 1910), Dhimbar, Coimbatore -Npd- (K). *Noble s.n.* (in 1962-63), seed and plant collections from six Badaga villages, Upper Nilgiri Hills—progeny: *J.D.S. 3954, 3955, 3965* -Gpd- (WIS); *Noble s.n.*, seed and plant collections from three Kurumba villages, Manjakombai area, Upper Nilgiri Hills—progeny: *J.D.S. 3949, 3950, 3953, 3956, 3960, 3961* -Gpd- (WIS); *Noble s.n.*, seed and plant from Kodomalai Estate, nr Coonor, Upper Nilgiri Hills—progeny: *J.D.S. 3952* -Gp- (WIS); *Noble s.n.*, seed from Irulas tribe, Caricure, Nilgiri Hills—progeny: *J.D.S. 3957, 3959* -Gpd- @, *3958* -Gp- (WIS); *Noble s.n.*, seed from Vilpatti, Pulni Hills-progeny: *J.D.S. 3963* -Gp- (WIS). MAHARASHTRA: *Tyson 30* (in 1953), seed from Poona—progeny: *J.D.S. 1703* -Np- (MICH, MO, UC, WIS). *Gentry 37440* (in 1954), seed from Poona—progeny: *J.D.S. 2538* -Np- (WIS). *Kelly s.n.* (in 1960), nr Ajanta, Aurangabad, *raj-giira* -Gp- (WIS). PUNJAB: *Stewart 1790* (in 1917), nr Pathankot, Ravi Valley -Np- (K). UTTER PRADESH: *von Hügel 158, 409* (in 1832), Mussoorie -Np- (W). *Ritchie s.n.* (ca 1840), Saharampore -Np- (E). *Madden 583* (ca 1845), Bashahr to Kumaon -Gp- (E). *Anonymous s.n.* (in 1846, 1848), Saharampore -Np- (K). *Strachey & Winterbottom 2b* (ca 1850), Kumaon -Np- (GH, K). *von Schlagintweit 9707* (in 1855), Nelong to Ussila, Garhwal -Np- (E). *Gamble 27404, 27432* (in 1898), Jaunsar, *chaulai* -Np- (K). *Bell s.n.* (in 1902), Banda, *ramdana* -Gp- (K). *Anderson s.n.* (in 1915), Mussoorie -Np- (E). *Huggins s.n.* (in 1952), seed from Harsil, Tehri Garhwal, *marcha*—progeny: *J.D.S. 1702* -Gp- (MICH, MO, WIS). *Lal s.n.* (in 1961), Mussoorie, *chaulai*—progeny: *J.D.S. 2845* -Gp- (WIS). *Andress s.n.* (in 1963), Mussoorie, *chaulai*—progeny: *Frenkel 889, 890* -Gd- (WIS).

KASHMIR. BALTISTAN: *von Schlagintweit 871* (in 1856), nr Skardo -Np- (L, UC); *von Schlagintweit 872*, nr Skardo -Np (BM, US); *von Schlagintweit 5789*, Kunes via Kiris to Neru -Np- (BM, US); *von Schlagintweit 5850*, Kunes via Kiris to Neru -Np- (E); *von Schlagintweit 6407*, Das via Goltere/Naugaum to Hasora/Astor -Np- (US). GILGIT: *Harlan 806* (in 1960), seed from Shimal garden nr Gupis, Teru, *gunerie*—progeny: *J.D.S. 3966* -Gp- (WIS). KASHMIR: *Thomson s.n.* (in 1848, 1849), s. loc. -Np- (K). *Aitchison s.n.* (in 1875), s. loc. *ganhar* or *sil* -Gpd- (K). *Polunin 300* (in 1956), Tangmarg -Gd- (MO, WIS); *Polunin 617*, Rezan, Sind Valley -Gpd- (MO, WIS); *Polunin 759*, Khanan, Wangat Nullah -Gd- (MO, WIS); *Polunin 804*, nr Miragund -Gpd- (MO, WIS); *Polunin 819*, *Srinagar* -Gpd- (MO, WIS). LADAK: *H. & R. von Schlagintweit 1771* (in 1856), Himis lamasery, nr Leh -Np- (BM); *H. & R. von Schlagintweit 1958*, Yugah to Leh -Np- (GH); *H. & R. Schlagintweit 12075*, Gures across Uri plain to Bandipur -Np- (GH).

NEPAL. *Wallich s.n.* (in 1821), s. loc. -Np- (K, P, W). *Janaki-Ammal 1482* (in 1948), seed from Makwanpur, nr Sirsagarhi—progeny: *J.D.S. 1495* -Gpd- (F, GH, MO, UC, US, WIS). *Nakao 194* (in 1953), seed from Tsumje, S slope of Sringi Himal—progeny: *J.D.S. 1713* -Gp- (MICH, MO, WIS); *Nakao 203*, seed from Thomje, Shiar Kola Valley—progeny: *J.D.S. 1714* -Gp- (MO, UC, WIS). *Tyson 20* (in 1953), Chainpur, Seti Valley, *marcha* -Gp- (MO).

SIKKIM. *Hooker s.n.* (in 1849), Lachen, Lachoong -Np- (K); *Hooker s.n.*, s. loc. -Npd- (BM, E, GH, K, W).

SOVIET RUSSIA IN ASIA. MARITIME TERRITORY: *Bohnhof s.n.* (in 1898-99), Lake Khanka -Np- (E, K).

AFRICA. UGANDA (not mapped). MASAKA: *Purseglove 1775* (in 1945), Kakuto, Buddu -Gp- (K). *Thomas 4494* (in 1946), Bawanga -Gp- (K).

Amaranthus cruentus

AMERICA. GUATEMALA. ALTA VERAPAZ: *J.D.S. 1265* (in 1947), nr Coban, *bledo* or *tses* -Gd- (DAO, F, GH, MO, UC, US, WIS). CHIMALTENANGO: *J.D.S. 1168* (in 1947), San Martin Jilotepeque, *bledo blanco* -Gpd- (DS, F, GAT, GH, TENN, UC, US, WIS); *J.D.S. 1240, 1267*, San Martin Jilotepeque, *bledo morado* -Gd- (DAV, MO, WIS). GUATEMALA: *J.D.S. 1176* (in 1947), San Juan Sacatepequez, *nigua negra* -Gpd- (DAO, GH, MO, US, WIS); *J.D.S. 1177*, San Juan Sactepequez, *nigua blanca* -Gp- (DAV, F, UC); *J.D.S. 3972* (in 1966), San Juan Sacatepequez, *nigua negra* -Gd- (WIS).

MEXICO. OAXACA: *Kaplan s.n.* (in 1954), seed from Mixtec village, Jicatepec, *chian*—progeny: *J.D.S. 2529* -Gp- @ (WIS). PUEBLA: *J.D.S. 1172* (in 1947), Acatlan, *alegria* -Gp- @ (GH, MO, UC, US, WIS). SINALOA: *Palmer 1718* (in 1891), Ymala, *guaute* -Gp- @ (US).

Amaranthus caudatus

AMERICA. ARGENTINA. SALTA: *Mintzer s.n.* (in 1938), seed from San Carlos, *quinoa*—progeny: *Hunziker s.n., 1085* -Gp- (G, GH, US). *Lovaglio 1449* (in 1941), seed from Cachi, *quinoa*—progeny: *Hunziker 2127* -Gp- (G, GH). *Hunziker 3003* (in 1943), San Carlos, *quinoa* -Gp- (MO). *Anonymous DEIP-17007* (in 1958), seed from Coronel Moldes experiment station, *chaclion*—progeny: *Grant 336* -Np- (WIS). TUCUMAN: *Hunziker 2550, 2555*, (in 1943), Colalao del Valle, *chaclion* or *quinoa de Castilla* -Gp- (G, K).

BOLIVIA. COCHABAMBA: *Cardenas 3512, 3514, 3515*, (in 1944), Cochabamba, *millmi* -Gp- (GH, US); *Cardenas s.n.* (in 1947), seed from Sacaba, *millmi*—progeny: *J.D.S. 1314, 1315* -Gpd- (UC, WIS). *Cutler s.n.* (in 1947), seed from Hacienda Chihuni, nr La Angostura, *millmi*—progeny: *J.D.S. 1179, 1241, 1298* -Gpd- (DAV, DS, F, GAT, GH, MO, TENN, UC, US, WIS). *Fuller s.n.* (in 1947), nr Cochabamba, *millmi* -Gp- (ILL). LA PAZ: *Kelly 1006* (in 1958), seed and plant from betw Chulumani & Irupana, *kwimi*—progeny: *J.D.S. 2540* -Gpd- (UC, WIS); *Kelly s.n.*, Chirca—progeny: *J.D.S. 2539* -Np- (WIS); *Kelly s.n.*, Tajma, Chulumani region, *quinoa*—progeny: J.D.S. 2542 -Np- (WIS). TARIJA: *Figueroa s.n.* (1941), Tarija, *coimi*—progeny: *Hunziker 2128* -Np- (GH).

ECUADOR. AZUAY: *Heiser 6554* (in 1966), nr Cuenca, *quinoa* -Gp- (IND, WIS).

PERU. ANCASH: *Bradford s.n.* (in 1956), Hacienda Vicas above Chancos, *achi* or *achita* or *cuipa* -Np- (USM). AYACUCHO: *Gade s.n.* (in 1964), nr Ayacucho, *achita* -Gd- (WIS). CUZCO: *Cook & Gilbert 256* (in 1915), Urubamba, *quihuicha* -Gp- (US). *Vargas s.n.* (in 1939), seed from Cuzco, *quihuicha*—progeny: *Hunziker 810* -Gp- (US); *Vargas s.n.* (in 1943), seed from Cuzco, *quihuicha*—progeny: *Cardenas 3513* -Gp- (GH). *Gade s.n.* (in 1964), Naihua, bottom of Apurimac gorge, *quihuicha* -Gd- (WIS). HUANCAVELICA: *Arevalo s.n.* (in 1948), seed from La Mejorada, *achita*—progeny: *J.D.S. 1283* -Gpd- (DAV, F, GH, MO, UC, US, WIS).

ASIA. AFGHANISTAN. Without province: *Griffith 4184* (about 1840), -Np- (GH).

CHINA. HUPEH: *Henry 7517* (about 1885), Changyang -Np- (K). KIRIN: *Komarov II-165* (in 1896), s. loc. -Np- (K). *Kozlow 14486* (in 1929), s. loc. -Np- (W). *Chen 369* (in 1931), nr Kirin -Np- (GH). LIAONING: *Webster 230* (in 1884), Mukden to Yalu River -Np- (K). SZECHWAN: *Yü 14479* (in 1937), Muli, Wachin—progeny: *Cowgill 2087* -Np- (E, GH). *Chang s.n.* (in 1948), seed from Mowhsien, progeny: *J.D.S. 1503* -Gp- (F, GH, MO, UC, US, WIS). YUNNAN: *Maire 319* (in 1906), Yunnansen -Np- (E). *Handel-Mazzetti 8479* (in 1915), Mekong Valley, 27½° N.L. -Np- (E). *Ten 1429* (in 1919), Pai Yen Ching -Gp- (W).

INDIA. Without province: *Edgeworth 85* (in 1844), NW India -Np- (K). HIMACHAL PRADESH: *Lace s.n.* (about 1900), Bashahr -Np- (E). MADRAS: *Noble s.n.* (in 1962), seed from Kurumba villages, Manjakombai, Upper Nilgiri Hills—progeny: *J.D.S. 3951, 3962* -Gp- (MO, WIS); *Noble s.n.*, seed from Vilpatti, Pulni Hills—progeny: *J.D.S. 3964* -Gp- (WIS). UTTAR PRADESH: *Buchanan-Hamilton 2028-2* (in 1813), Beloya -Np- (E). *Jameson 776* (in 1845), Mussoorie -Np- (K). *Madden s.n.* (about 1850), Mussoorie -Np- (E). *Strachey & Winterbottom 2a* (about 1850), Kumaon -Np- (GH). *King s.n.* (in 1869), nr Mussoorie -Np- (L). *Anderson s.n.* (in 1915), Mussoorie -Gp- (E).

KASHMIR. BALTISTAN: *von Schlagintweit 5787* (in 1856), NE of Skardo -Np- (US).

NEPAL. *Wallich s.n.* (in 1821), s. loc. -Np- (G, K, P). *Janaki-Ammal 1481* (in 1948), seed from Makwanpur, nr Sirsagarhi—progeny: *J.D.S. 1505* -Gp- (MO, UC, WIS). *Nakao 188, 191, 201, 205* (in 1953), seed from Ulleri, SW slope of Annapurna—progeny: *J.D.S. 1707-1710* -Gp- (F, GH, MICH, MO, UC, US, WIS); *Nakao 204*, seed from Ghasa, W slope of Annapurna—progeny: *J.D.S. 1712* -Gp- (MICH, MO, WIS); *Nakao 210*, seed from Sikha, SW slope of Annapurna—progeny: *J.D.S. 1711* -Gp- (WIS).

AFRICA. ETHIOPIA: (not mapped). ILUBABOR: *Meyer 8905* (in 1964), Tukle, nr Teppi -Gp- (WIS). KEFA: *Anderson & Getachew s.n.* (in 1957), nr Jimma, *lishalisho* or *kettila* -Gdp- (WIS). *Mengesha s.n.* (in 1957), Missan Tefferi -Gp- (WIS).

NOTES ON WOODY RUBIACEAE OF TROPICAL AMERICA

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ABSTRACT

Two sections, 12 species, and one form from the neotropics are described as new to the *Rubiaceae*. These include *Faramea* sect. *Integrisepta*, F. sect. *Uniflora*, *Chomelia chambersii*, *C. psilocarpa*, *Dukea trifoliata*, *Faramea persistisepta*, *F. platycarpa*, *F. talamancarum*, *F. acutifolia*, *F. uniflora*, *Psychotria gatunensis*, *P. ostaurea*, *P. woytkowskii*, *Rondeletia dukei*, *R. hameliifolia*, and *Rudgea horquetensis*. In addition, the range of *Faramea trinervia* is extended to include Panama.

In studying arborescent and suffrutescent *Rubiaceae* from the American tropics a number of novelties were encountered.

1. *Chomelia* **chambersii** Dwyer & Hayden, sp. nov.

Arbores parvae, ramulis laevibus teretibus. *Folia* stipulis deciduis triangularibus basi connatis, saepe crebra et apice ramulorum subfasciculata, petiolis gracilibus, 1-2.5 cm longis, ca 1.5 cm latis, pilosis; lamina elliptica vel late elliptica, 5-12 cm longa, 2-6 cm lata, apice obtusa vel subrotundato-obtusa tunc ultime acuminata, acumine ad 1.5 longo, ca 0.6 cm lato, saepe falcato, basi acuta vel cuneata, rare obtusa, plerumque inaequilateralis, membranacea vel papyracea supra sparse pilosa subtus pilosior, venis lateralibus alternatis, ca 12, arcuato-ascendentibus, conspicue ramosis prope margines, venis marginalibus patulo-reticulatis. *Flores* non visi. *Inflorescentiae* (hic in fructu) axillares vel terminales?, ad 13 cm longae, pedunculo ad 9 cm longo, piluloso, ramis terminalibus bene proximis, ascendentibus vel forte arcuato-divergentibus vel flabellate reflexis, ramulis plerumque geminatis, brevibus, 1-2 cm longis, saepe inaequilateralibus, cicatricibus fructuum ovalibus conspicuis unilateraliter et seriatim dispositis. *Fructus* sessiles, elliptici, ca 1 cm longi, ad 0.5 cm lati, obtusi, laeves, seminibus solitariis, endospermo biporoso (trans. sect.).

PANAMA. CHIRIQUÍ: Comarca del Baru, area nr Puerto Armuelles, betw Cañazo & Cocos, *Stern & Chambers 144* (holotype MO). DARIEN: 1-3 mi SE of Santa Fe on Pan Am Hwy, *Duke 4119* (MO); Río Chico across Boca Tesca along top of ridge, *Duke 5220* (MO); Santa Fe, *Duke 8389* (MO); Río Balsa betw Quebrada Chusomocatre & Río Areti, *Duke 8709* (MO); vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 825* (MO). SAN BLAS: Nakka, *Dwyer 4567* (MO).

The Stern & Chambers collection (*144*), originally identified and distributed as *Hamelia axillaris* Sw., is described by the collectors as having fruit clusters which resemble those of *Viburnum*. A wood sample of the same collection is deposited at Yale University (Yale wood collection #*51638*). Field observations suggest that the tree is common in Darien. Duke records that the tree is used for canalete and handles and that the common name is *taaplizo*.

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2. *Chomelia* **psilocarpa** Dwyer & Haden, sp. nov.

Frutex scandens, ramis glabris laevibus. *Folia* stipulis triangularibus vel subulatis, ad 0.9 cm longis, elongato-acuminatis, basi ca 3.5 mm latis, laevibus glabrescentibus diffuso-pilosulis, pedicellis 0.7-2 cm longis, appresso-subhirsutis; lamina elliptica, 6.5-13 cm longa, 2.5-6 cm lata, apice primo acuta tunc acuminata, acumine ad 1 cm longo, ultime apiculato, apicula ca 1 mm longa, basi attenuato-acuta, papyracea, supra glabrescens, ciliis brevibus albis deciduis, subtus ciliolatis (praeter venas elongato-appresso-pilosas) ciliisque brevioribus et seriatim dispositis, axillis venarum lateralium dense barbatis, costa subtus prominula, venis lateralibus 6, alternis fortiter arcuatis. *Flores* non visi. *Inflorescentiae* axillares cymoso-paniculatae, ad 9 cm longae, ca 6 cm latae, pedunculo 4-7 cm longo, ca 1.5 mm lato, dense appresso-piloso, ramulis primariis 2, terminalibus ascendentibus, 1-7 cm longis, bifurcatis, eis iterum plerumque ramosis, bracteis bracteolisque lineari-subulatis glabrescentibus, ad 3 mm longis, bracteis pluribus, ad apicem pedicellorum circulatim dispositis. *Fructus* sessiles vel pedicellati, pedicellis ad 2 mm longis, elliptici, ca 1 cm longi, ad 0.6 cm lati, obtusi, in sicco subnigri dense pilosi, lobulis calycis 4, hic persistentibus conspicue erectis, lineari-subulatis vel lineari-ligularibus, 2 brevioribus 2-3 mm longis, 2 longioribus 5-6 mm longis, exocarpio carnoso, dense appresso-pilosulis, endospermo corneo lueto biporoso (trans. sect.).

PANAMA. CANAL ZONE: Barro Colorado I, SE shoreline from Lab, *Hayden 143* (holotype MO).

The new species is immediately distinguishable by being a vine as well as by bearing densely pilulose fruits with elongate persistent calycine lobes. A longitudinal section of the fruit (here collected green) suggests that the embryo is pendulous; the biporous endosperm, characteristic of *Chomelia* is readily seen in cross-section.

3. *Dukea* **trifoliata** Dwyer & Hayden, sp. nov.

Frutex ad 3 m altus, ramulis late canaliculatis, dense appresso-pilulosis. *Folia* stipulis ovato-triangularibus, ad 2 cm longis, obtusis, appresso-pilulosis, ciliis basi subturgidis, longitudinaliter costatis, foliis 3 per nodum instructis, petiolis 2-4 cm longis, ca 0.3 cm latis; lamina elliptica vel obovato-elliptica, 18-25 cm longa, 6-8.5 cm lata, apice subcuneata tunc ultime cuneata, acumine late triangulari, basi cuneata vel acuta saepe paulo inaequilateralis, rigide papyracea, supra diffuso-appresso-pilosa, infra forte pilosa, venis lateralibus ca 17, lato-arcuatis, subtus prominulis, leviter reticulata. *Inflorescentiae* (hic in fructu) terminales, cymoso-paniculatae, hic 80 cm longae, 3 cm latae, pedunculo ad 3 cm longo, dense aureo-piloso, ramis regulariter geminatis, inferioribus ad 1 cm longis, ca 2 cm distantibus, ramulis superioribus paucis brevissimis apice fasciculatis, cymulis semper terminaliter dispositis, bracteis bracteolisque subulatis dense aureo-pilosis. *Flores* non visi praeter calycem persistentem, calyce brevi urceolato, dentibus minutis 4. *Fructus* (hic

immaturi) rotundi, ca 0.7 cm longi, in sicco nigri modeste pilosi, biloculatum, septo integro et 2 medianas placentas ferente, seminibus parvis multis foveolatis.

Panama. coclé: El Valle de Antón, edge of potato farm above village, ca 2000 ft elev, *Dwyer 1933* (holotype MO).

Recently I described the genus *Dukea* (Ann. Missouri Bot. Gard. **53:** 360-367, 1966) with four species from Panama and one from Colombia. This species is the easiest to distinguish as the leaves are disposed in threes at a node.

4. *Faramea* **persistisepta** Dwyer & Hayden, sp. nov.

Arbores?, ramulis laevibus glabris, nodis leviter dilatatis. *Folia* stipulis late cupulatis, ad 1.5 mm longis, basi connati?, marginibus late undulatis, pedicellis 0.5-2 cm longis, laevibus glabrescentibus; lamina lato-elliptica vel elliptica (minoribus subcircularibus), apice rotundato-obtusa, basi acuta vel cuneata, abrupte acuminata, acumine ad 1 cm longo, ad 1 cm lato, crasso-membranacea vel papyracea glabra, costa prominula, venis lateralibus ca 8, leviter prominulis, vix arcuatis. *Inflorescentiae* terminales cymoso-paniculatae, ad 8 cm longae, ad 5 cm latae, pedunculo ad 2.5 cm longo, ca 0.2 cm lato, glabro, ramis primariis bene distantibus, inferioribus geminatis, ca 1 cm longis, ramis superioribus 1-2 vel 4, cymulis ternate dispositis, bracteis connatis sic patulo-cupuliformibus, apice minuto-apiculatis. *Flores* hypanthio subrotundo, ca 1 mm longo; calyx urceolatus, ca 1 mm longus, glaber, dentibus 5 minutis, ad 0.2 mm longis, acutis; corolla tubo cylindrico, ca 4 mm longo intus dense piloso, lobis 4-5, ca 3.5 mm longis; antherae ca 1 mm longae, filamentis elongatis, ca 3 mm longis, prope orem tubi affixis; ovarium biloculatum, septo crasso, integro, ovulis 2, basaliter affixis, pyriformibus, hic ca 0.5 mm longis stigmatum patulis. *Fructus* depresso-globosi, ad 5 mm longi, ca 6 mm lati, superficie longitudinaliter canaliculati, glabri, cicatrice calycis circulare, septo intus integro.

Bolivia. sara: Santa Cruz, 450 m elev, *Steinbach* 7253 (MO); Santa Cruz, submonte del Río Surutu, 400 m elev, *Steinbach* 7238 (holotype MO).

The fruit, while obviously that of *Faramea*, e.g. in being wider than long, is anomalous as the septum does not disappear in the fruit. The septum is rigid and cannot be forced apart easily without a dissecting needle. This is probably the first species of *Faramea* to be described in which the ovary and the fruit possess a complete septum. On the basis of this a new section of the genus seems warranted: thus Sectio **integrisepta** Dwyer & Hayden, sect. nov., floribus fructibusque septo integro notata. Type species, *F. persistisepta* Dwyer & Hayden.

5. *Faramea* **platycarpa** Dwyer & Hayden, sp. nov.

Arbores parvae, ramulis teretibus laevibus. *Folia* stipulis in gracilem elongatam vaginam junctis, vagina ad 1 cm longa, ca 0.3 cm lata, apice bifida, lobo utroque elongato-setoso, seta ad 7 mm longa; petioli graciles, ad 0.5 cm longi; lamina angusto-elliptica, 4-10.5 cm longa, 1-2.8 cm lata, apice elongate attenuato-

acuminata, acumine ad 2 cm longo ad 0.3 cm lato ultime obtuso, basi acuta, in sicco viridis tenui-papyracea, costa gracili prominula, venis lateralibus 10-12, late arcuatis sed mox venae marginali undulatae a margine ca 4 mm distanti junctis, areolis patulis reticulatis. *Inflorescentiae* terminales sessiles glabrae vel ramis 2-3 (-5) basaliter dispositis vel pedunculo ad 1.5 cm longo, pedicellis terminalibus ascendentibus, umbellate dispositis, ca 0.8 cm longis. *Fructus* magne compresso-rotundi, ca 8 cm longi, ca 1.6 cm lati.

ECUADOR. Napo-Pastaza, 11 mi N of Archidona Trail betw Baeza & Tena, 3000 ft elev, *Owenby 2711* (holotype MO).

6. *Faramea talamancarum* Standley f. **acutifolia** Dwyer, f. nov.

Lamina foliorum apice elongato-acuminata, acumine ad 1 cm longo, ultime acutissimo.

PANAMA. DARIEN: Paya, Río Paya, trail from Paya to Pucro, *Stern, Chambers, Dwyer & Ebinger 230* (holotype MO).

Faramea talamancarum was originally described from M. A. Carleton's collection (*145*) from the Talamanca Valley, Bocas del Toro, Panama; it is also known from San Ramon, Guanacaste, Costa Rica. The new form differs in having elongate and attenuate-acuminate leaves which are shaped more like a leaf of *Salix* than obovate or oblong as in the typical material.

7. *Faramea trinervia* K. Schum. & J. D. Sm., Bot. Gaz. **31:** 115, 1901.

PANAMA. BOCAS DEL TORO: *Punta Peña, Lewis et al. 2145* (MO).

The field notes describe this collection as about two meters tall. The foliage seems to match the general description of *F. trinervia* K. Schum & J. D. Sm. except the blades are not sessile but are borne on petioles up to 1 cm in length. The intervenal areas of the Panamanian collection are distinctly bullate which may have resulted from the drying process. Standley (Flora of Costa Rica, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 1297, 1938) states that *F. trinervia* is endemic to the forests of Boca Zhorquin, Talamanca, Costa Rica, thus making the above collection a noteworthy range extension.

The following is a description of the fruit, previously unknown: *fruit* depressed-ovate, much wider than long, up to 0.8 cm long, 1.5 cm wide, the remnants of the calycine lobes minute or wanting, the calycine scar scarcely distinguishable, a thin and scarcely elevated septal ridge extending for about 0.5 cm on each side from the scar, then evanescent, the surface glabrous, smooth except minutely farinose-papillate.

8. *Faramea* **uniflora** Dwyer & Hayden, sp. nov.

Frutex ad 2 m altus, ramulis gracilibus, glabrescentibus. *Folia* stipulis plerumque connatis amplexicaulibus, vagina ad 9 mm longa, minuto-apiculata, apicula ad 2 mm longa, saepe partim decidua, pedicellis deficientibus vel ad 0.5 cm longis;

lamina in sicco viridis anguste elliptico-oblonga, 4-9 cm longa, 1.3-2.5 cm lata, apice elongato-cuspidata, saepe falcato-cuspidata, cuspide ad 1.3 cm longa, basi acuta membranacea, puberula, ciliolis minutis albidis seriatim dispositis, subtus glabrescentibus, costa vix prominula, venis lateralibus 15-20, late arcuatis prominulisque. *Flores* sessiles solitarii terminales in ramulis brevibus axillaribus dispositi, azurei, ad 2 cm longi, bracteis (superioribus foliis) fortiter ascendentibus erectis, hypanthio ca 0.75 mm longo, glabro; calyx vix urceolatus, ca 0.75 mm longus, dentibus 4, minutis acutis; corolla tubo late cylindrico, ca 15 mm longo, ad 6 mm lato, intus glabro, basi paulo latiore, lobulis 4, ca 6 mm longis, reflexis; antherae angusto-oblongae, ca 4.5 mm longae, ca 1 mm latae, obtusae, filamentis ca 3 mm longis, prope basin tubi affixis; stylus ca 1.2 mm longus, lobis stigmatum erectis linearibus; ovarium ovulis 2 connatis baseliter affixis, septo non integro, fortiter reducto.

Fructus globosi, ca 1.5 longi, seminibus solitariis, magnis.

Peru. amazonas: Mendoza, 1600 ft elev, *Woytkowski 8309* (holotype MO).

As the specific name suggests, the flowers are solitary. The uniflorous condition has not been reported for the genus. Noteworthy, too, is the extreme reduction of the ovarian septum. The flowers are blue and the corolla tube is unusually wide.

We propose a new section for *Faramea:* Sectio **Uniflora** Dwyer & Hayden, sect. nov., floribus solitariis distinguenda est. Type species *F. uniflora* Dwyer & Hayden.

9. *Psychotria* **gatunensis** Dwyer & Hayden, sp. nov.

Arbores ad 7 m altae, ramulis teretibus laevibus glabris. *Folia* stipulis caducuis, cicatricibus stipularum conspicuis, ad 2 mm longis, petiolis ad 1.5 cm longis, saepe alatis (basi laminae decurrente), ala ad 1.5 mm lata; lamina elliptica, obovato-elliptica vel obovato-rotunda, 16-24 cm longa, 8-12 cm lata, apice late cuneata, basi attenato-cuneata, crasso-papyracea supra glabra, subtus minute rufo-pubescente, venis lateralibus late arcuatis subtus prominulis. *Inflorescentiae* terminales patulae subpyramidato-paniculatae, ad 11 cm longae, ad 10 cm latae, pedunculo ad 3 cm longo, ad 0.35 cm lato, conspicue costato, rufo-villosulo, ramis primariis (hic in gemmis) basalibus, ad 3.5 cm longis, ramis secundariis 2-3 flores terminales ferentibus, vel ramis secundariis 2-3, utroque ramulo 2-3 flores ferente. *Flores* integros non vidimus; calyx coronarius persistens dentibus 2-2.5 mm longis. *Fructus* pedicellis brevibus, ad 0.4 cm longis, elliptici, 1.3-1.5 cm longi, 0.6-0.7 cm lati, 5-costati, sparse pubescentes, calyce persistente coronario cupulato pubescente, ad 1.5 cm longo, ad 3 mm lato.

Panama. canal zone: Gatun Locks & Gatun Lake, nr Maru Towers, *Johnston 1554* (holotype MO).

The pedicel scars on some of the secondary and tertiary branches of the fruiting inflorescence suggest that the flowers were originally sessile, developing pedi-

cels in fruit. In the fruit the endocarp pore which characterizes most species of *Palicourea*, and perhaps *Cephaelis* is absent. The deep furrows of the ventral surface of the endosperm suggests *Psychotria undata* Jacq. and *P. grandis* Sw., both of which are not uncommon on the Atlantic side of the Canal Zone. The fruits, while probably immature, are extraordinarily large for a species within the Central American range of the genus. Unfortunately stipules were not seen.

10. *Psychotria* **ostaurea** Dwyer & Hayden, sp. nov.

Arbores ad 8 m altae, ramulis laevibus. *Folia* (unum vidimus) stipulis triangularibus, petiolo ad 3.5 cm longo, minutissimo-puberulo; lamina elliptico-rotunda, hic 27 cm longa, 15 cm lata, apice breviter acuminata, basi cuneata, lamina rigido-papyracea, costa subtus supraque prominula, venis lateralibus ca 14, fortiter arcuato-ascendentibus, supra glabra, subtus puberula in venis, areolis supra evanescentibus tam patulo-reticulatis. *Inflorescentiae* patulae cymoso-paniculatae, ad 12 cm longae, ca 8 cm latae, pedunculo ad 4.5 cm longo, minute puberulo, ramis primariis quadrate dispositis, ad 6 cm longis, fortiter ascendentibus, ramis secundariis paucis patulis, bracteolis minutis divaricatis. *Flores* pedicellis nullis vel ad 2 mm longis; hypanthium quadrangulare, ca 1 mm longum; calyx coronarius cupulatus, ca 1 mm longus, undulato-truncatus, dentibus nullis, in sicco pallido-luteus; corolla ca 1.5 cm longa, tubo cylindrico deorsum vix turgido glabro, lobis 5, crassis quam tubo longioribus, obtusis reflexis; antherae 5 vix exsertae lineari-ellipticae, ca 5 mm longae, filamentis brevibus, propre apicem tubi affixae; ovarium septo crasso, ovulis 2 basalibus, stigmatibus subulato-sagittatis.

PANAMA. BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *von Wedel 1461* (holotype MO).

Presumably Standley intended to describe this as a new species of *Coussarea*, as the herbarium label of *von Wedel 1461* suggests. The thick median septum of the ovary, separating the 2 basally attached ovules, and the general 5-merous condition of the floral whorls confirm that it is a *Psychotria*. The leaves are strikingly large. The specific name *ostaurea* (mouth of the bull) refers to the Province of Bocas del Toro.

11. *Psychotria* **woytkowskii** Dwyer & Hayden, sp. nov.

Arbores?, ramulis teretibus laevibus glabris, nodis 3-3.5 cm distantibus. *Folia* stipulis amplexicaulibus basi connatis, rectangularibus utraque stipula setis 2 lateralibus ca 2 mm longis ornata, aureo-pubescentibus, petiolis ad 6 mm longis, supra pubescentibus glabris; lamina elliptica, 7-9 cm longa, 3-4.5 cm lata, apice rotundo-subabrupto-acuminata, acumine subtriangulari, ad 0.75 cm longo, basi acuta, rigide papyracea, supra minute puberula (praeter costam farinoso-pilosam), ciliolis seriatim dispositis subtus aureo-piloso in costa et basi venarum, in sicco viridis, costa supra subplana, subtus vix prominente, venis lateralibus subprominentibus, ca 10, luteis, venis intermediis irregularibus conspicuis, areolis leviter reticulatis. *Inflorescentiae* terminales contracto-cymoso-paniculatae, ad 4 cm longae, ad 2.5

cm latae, pedunculo nullo vel ad 1 cm longo, cymulis dense compactis. *Flores* parvi (hic immaturi), sessiles hypanthium calyxque campanulatum, ad 1 mm longum, pubescens, dentibus 5, minutis; corolla tubo (hic immaturo) brevi extus pubescente, intus basi pubescente, lobis ad 1.5 mm longis; antherae 5, obtusae, filamentis gracilibus; ovarium septo crasso, ovulis 2 basaliter affixis.

PERU. AMAZONAS: Rodriquez de Mendoza, *Woytkowski 8190* (holotype MO).

The thick septum of the 2-celled ovary, with a single ovule in each locule, suggests both *Palicourea* and *Psychotria*. The fact that the stipules are basally connate and bear two lateral awns per stipule favors placing it in the former. The flowers, at least in the dry state, are tinged with purple, a fact which also suggests *Palicourea*. However, considering that the inflorescence is markedly contracted, we are electing to place it in *Psychotria*. The new species is named in honor of the late Felix Woytkowski who has contributed so much to our knowledge of South American plants, particularly those of Peru.

12. *Rondeletia* **dukei** Dwyer & Hayden, sp. nov.

Frutex?, ramulis in sicco leviter purpureis glabris sed supra nodos ciliolatis. *Folia* stipulis triangularibus, ad 0.6 cm longis, ad 0.4 cm latis, acutis, glabrescentibus vel aureo-pubescentibus, petiolis 1-1.6 cm longis, gracilibus in sicco nigris, glabris; lamina elliptico-oblonga, 6-8 cm longa, 4-5 cm lata, apice obtusa vel rotundo-obtusa, basi cuneata, rigide membranacea, glabra, costa prominula, venis lateralibus patulo-reticulatis. *Inflorescentiae* terminales vel axillares, spiciformae, pedunculo ad 6.5 cm longo, ca 1 mm lato, glabro, minute farinoso, floribus vel sessilibus solitariis vel in fasciculos paucifloros moderate distantes dispositis. *Flores* albi pedicellati, pedicellis ad 0.3 cm longis; hypanthium subrotundum, ca 1.5 mm longum, lobis calycis 5, oblongo-rotundis, ca 2 mm longis, floribus inferioribus lobo uno aut lobis duobus saepe in latam foliosam laminam amplificatis, lamina loborum ovata, ad 4 cm longa, obtusa, in sicco lutea; corolla tubo ca 2 mm longo, apice intus sparse ciliolato, extus dense puberulo, lobis 5, 2-3 mm longis, imbricatis obtusis anthesi patulis; antherae 5, oblongae, 1-1.5 mm longae, versatiles filamentis inaequalibus. *Fructus* non visi.

PANAMA. DARIEN: Río Pirre, *Duke 8329* (holotype MO).

The one or two large and flaring calycine lobes, found only on the lowermost flowers of the inflorescence, readily distinguishes the new species. It is named in honor of the collector, Dr. James Duke. He lists the common name as *madrono*.

13. *Rondeletia* **hameliifolia** Dwyer & Hayden, sp. nov.

Suffrutex ad 8 m altus, ramulis teretibus, diffuso-albido-pilosis, nodis saepe subturgidis (partim reliquis stipularum). *Folia* stipulis triangulari-subulatis, ad 0.75 cm longis, apice fortiter acutis extus albido-puberulo, intus rufo-pubescente, breviter basi connatis, petiolis gracilibus, ad 0.5 cm longis; lamina elliptica vel rotundo-elliptica, 5-9 cm longa, 2.3-3.5 cm lata, apice cuneata, late

acuminata, basi cuneata, rigido-papyracea, supra infraque pilosa, ciliis supra albidis paucis appressis, subtus in venis crebre dispositis, costa prominula, venis subtus prominulis, venis lateralibus 6-7, fortiter arcuato-ascendentibus. *Inflorescentiae* terminales, cymoso-paniculatae, 4-6 cm longae, ad 6 cm latae, pedunculo ad 1-2 cm longo, ramis primis geminatis, paucis bene distantibus (0.5-1.2 cm) fortiter distantibus, ramulis ternate supra medium ramorum dispositis, cymulis paucifloris vel saepe floribus solitariis, bracteis persistentibus, triangulari-subulatis, aureo-pubescentibus, bracteolis persistentibus subulatis aureo-pubescentibus. *Flores* albi, sessiles vel pedicellati, pedicellis ad 3 mm longis, aureo-pubescentibus; hypanthium rotundum, ca 2 mm longum, dense aureo-pubescens, lobis calycis 5, oblongis vel triangulari-subulatis, subaequalibus, ca 1.5 mm longis, apice obtusis; corolla tubo salverforme, ad 5 mm longo, apice ca 1.1 mm lato, in vivo intus luteo, vix annulari-marginata, lobis 5 obtuso-rotundis, ca 4 mm longis, apice rotundo-obtusi, antherae 5, lineari-oblongae, ca 2 mm longae, filamentis brevibus, proxime medium tubae affixis; ovarium biloculatum, septo crasso integro, ovulis multis subtrapeziformibus. *Fructus* non visi.

PANAMA. VERAGUAS: Santiago, *Dwyer 1350* (holotype Mo).

The new species seems closely related to *Rondeletia costaricensis* Standley but differs in having triangular-subulate stipules in contrast to the subrotund stipules of Standley's species. In addition the leaf-blades are more numerous, more strongly ascending, and are more moderately pilose.

14. *Rudgea* **horquetensis** Dwyer & Hayden, sp. nov.

Arbores ad 7 m altae, ramulis laevibus glabris rimosis. *Folia* stipulis brevibus, vagina integra, ca 2 mm longa, pedicellis gracilibus, ad 1.2 cm longis, ca 0.1 cm latis; lamina anguste elliptica vel elliptica, ad 8.5 cm longa, 2-3.5 cm lata, plerumque angusto latere acuminata, acumine brevi, basi acuta vel cuneata, discolor et supra plus brunnea vix rigide papyracea, omnino glabra, venis lateralibus ca 6, subtus prominulis. *Inflorescentiae* terminales paniculatae, ad 7.5 cm longae, ad 5 cm latae, pedunculo gracili, ca 1.5 mm lato, ad 3 cm longo, ramis ca 6, inferioribus ad 2.5 cm longis, ramulis tertiis paucis, cymulis pauco-floriferentibus, aliquibus terminalibus, aliquibus supra medium ramulorum distantibus, bracteis bracteolisque minutis subulatis glabris. *Flores* ad 2 cm longi, sessiles vel vix pedicellati; hypanthium subrotundum, ca 2 mm longum, glabrum; calyx cupuliformis, dentibus 5, minutis; corolla in gemma saepe falcata, apice clavata et obtusa, tubo erecto, ad 2 cm longo, lobis 5 reflexis, ad 6 mm longis; antherae sagittatae, ca 4 mm longae, apice attenuato-acuminatae, filamentis brevibus; ovarium biloculatum, septo crasso, ca 0.5 mm lato, ovulis obpyriformibus, ca 1 mm longis, a basi ovarii abeuntibus. *Fructus* non visi.

PANAMA. CHIRIQUÍ: Cerro Horqueta, 6500 ft alt, *von Hagen & von Hagen 2156* (holotype NY).

While convincing arguments may be advanced to support placing this species in *Psychotria*, it appears to belong to *Rudgea*. Its folded C-shaped ovules (cross-section), very short corolla lobes and sagittate anthers point to a position in *Rudgea*. The thickened ovarian septum precludes it being placed in *Coussarea*, a genus which it resembles superficially.

CHROMOSOME NUMBERS OF CLAYTONIA VIRGINICA IN THE ST. LOUIS, MISSOURI AREA

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ABSTRACT

Chromosome numbers of $2n = 22$, 23, 24, 25, 26, 27, 29, 30, 31, 32, 33, 34, 35, 36, and 37 are reported for *Claytonia virginica* L. from the St. Louis, Missouri area. Those plants with $2n = 24$ and 30 are by far the most frequent. Morphologically the species separates into two groups: plants having narrow leaves which are characteristic of the lower polyploid cytotypes, and those having broad leaves which are typical of the higher polyploid races.

The widespread diversity of chromosome numbers from $2n = 12$ to 191 is well documented for the portulacaceous species *Claytonia virginica* L. (Rothwell, 1959; Rothwell & Kump, 1965; Lewis, 1967; Lewis et al., 1967), although the study of many plants from a single area has only been attempted in eastern Texas (Lewis, 1962). The purpose of this research was to learn what chromosomal and morphological diversity existed for *C. virginica* in the St. Louis area.

During the spring months of 1966 and 1967, flower buds were removed from plants of 28 populations in St. Louis and St. Louis County. Pollen mother cell meiosis was observed for 175 plants, a sample considered large enough to illustrate diverse trends in the species if indeed they existed in the area. Cytological procedures followed those of Lewis (1962) and voucher specimens for each population were collected and are housed in the Missouri Botanical Garden herbarium (MO).

RESULTS AND DISCUSSION

Below are listed the chromosome numbers found for varying numbers of plants sampled at random from the 28 populations. The exact locality for each population is given together with the diploid number of plants (frequency in parenthesis) and the meiotic configurations generally at metaphase I or more rarely at anaphase I or metaphase II. Occasionally a count was confirmed by somatic divisions, but these are not indicated. Only two plants were found to be aneusomatic, i.e. with chromosome number varying intra-individually (Lewis, 1962); apart from their listing below and notation in Fig. 1, these plants will not be considered further.

A. St. Louis Co, 380 St Louis St, Florissant, *Suda 12:* **2n = 30**(6), **31**(3), **33**(1)—6 plants 15_{II}, 3 plants $15_{II}+1_{I}$, 1 plant $16_{II}+1_{I}$. [1967]

B. St Louis Co, nr jct of Old Halls Ferry Rd & Parker Rd., Black Jack, *Suda 16:* **2n = 30**(5), **31**(3), **32**(1), **33**(1)—5 plants 15_{II}, 3 plants $15_{II}+1_{I}$, 1 plant 16_{II}, 1 plant $16_{II}+1_{I}$. [1967]

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C. St. Louis Co, 1370 Criterion Ave, Spanish Lake, *Suda 11:* **2n = 24**(5), **30**(1), **34**(1)—5 plants 12_{II}, 1 plant $12_{II}+6_{I}$, 1 plant 17_{II}. [1967]

D. St Louis Co, jct of Estelle Ave & Harvey Ave, Ferguson, *Suda 13:* **2n = 24**(1), **25**(2), **26**(7)—1 plant 12_{II}, 2 plants $12_{II}+1_{I}$, 1 plant $11_{II}+4_{I}$, 3 plants $12_{II}+2_{I}$, 3 plants 13_{II}. [1967]

E. St. Louis Co, 10045 Viscount Dr, Moline Acres, *Suda 9:* **2n = 30**(6), **31**(4)—6 plants 15_{II}, 4 plants $15_{II}+1_{I}$. [1967]

F. St Louis Co, 208 Midlothian Rd, Larimore, *Suda 10:* **2n = 22**(8), **23**(2)—8 plants 11_{II}, 2 plants $11_{II}+1_{I}$. [1967]

G. St Louis Co, 3529 Calvert Ave, St John, *Suda 14:* **2n = 30**(4)—4 plants 15_{II}. [1967]

H. St Louis Co, 3724 Avondale Ave, Arbor Terrace, *Suda 15:* **2n = 24**(2), **25**(2), **26**(1), **27**(1), **29**(1), **30**(2), **32**(1)—2 plants 12_{II}, 2 plants $12_{II}+1_{I}$, 1 plant 13_{II}, 1 plant $13_{II}+1_{I}$, 1 plant $12_{II}+5_{I}$, 1 plant $12_{II}+6_{I}$, 1 plant $1_{IV}+10_{II}+6_{I}$, 1 plant $12_{II}+8_{I}$. [1967]

I. St Louis, Terminal RR betw W Florissant & Bdwy, *Lewis 6607:* **2n = 24**(1)—1 plant 12_{II}. [1966]

J. St Louis, nr Mark Twain Expressway, O'Fallon Pk, *MacBryde 23:* **2n = 30**(2), **32**(1), **35**(1)—1 plant 15_{II}, 1 plant 15_{II} & $14_{II}+2_{I}$, 1 plant $15_{II}+2_{I}$, 1 plant $16_{II}+3_{I}$. [1966]

K. St Louis Co, 12824 Ladue Rd, *MacBryde 18:* **2n = 22**(1), **23**(3), **24**(1)—1 plant 11_{II}, 3 plants $11_{II}+1_{I}$, 1 plant 12_{II}. [1966]

L. St Louis Co, Ladue Rd, 0.7 mi W of Price Rd, Ladue, *MacBryde 15:* **2n = 30**(2), **31**(1), **32**(2)—1 plant $14_{II}+2_{I}$, 1 plant 15_{II}, 1 plant $15_{II}+1_{I}$, 2 plants 16_{II}. [1966]

M. St Louis Co, John Burroughs School, Ladue, *MacBryde 14:* **2n = 24**(2)—2 plants 12_{II}. [1966]

N. St Louis Co, 332 N Meramec Ave, Clayton, *MacBryde 17:* **2n = 30**(4)—4 plants 15_{II}. [1966]

O. St Louis Co, 601 S. Brentwood Blvd, Clayton, *MacBryde 9:* **2n = 23**(1), **24**(10), **25**(2), **26**(1), **30**(1), **23-25** (1, aneusomatic)—1 plant $11_{II}+1_{I}$, 10 plants 12_{II}, 2 plants $12_{II}+1_{I}$, 1 plant $12_{II}+2_{I}$, 1 plant $12_{II}+6_{I}$, 1 plant $11_{II}+1_{I}$ (2 cells), 12_{II} & 12+12 (9 cells) & 12_{II} & 1_{I} (2 cells). [1966, 1967]

P. St Louis Co, Oak Knoll Pk, Clayton, *MacBryde 10:* **2n = 24**(3)—3 plants 12_{II}. [1966]

Q. St Louis Co, Washington Univ campus, *Lewis 6688:* **2n = 29**(2), **30**(2), **32**(1), **36**(2)—2 plants $14_{II}+1_{I}$ (+0-1 fragment), 2 plants 15_{II}, 1 plant 16_{II}, 2 plants $17_{II}+2_{I}$. [1966]

R. St Louis Co, 6355 Pershing Ave, University City, *MacBryde 24:* **2n = 24**(13), **37**(2)—1 plant $11_{II}+2_{I}$, 12 plants 12_{II}, 1 plant $16_{II}+5_{I}$ & $18_{II}+1_{I}$, 1 plant $17_{II}+3_{I}$. [1966, 1967]

S. St Louis, betw St Louis Zoo & Art Museum, Forest Pk, *MacBryde 11:* **2n = 24**(4), **25**(2)—4 plants 12_{II}, 2 plants $12_{II}+1_{I}$. [1966]

T. St Louis, N of Jewel Box, Forest Pk, *MacBryde 22:* **2n = 24**(4)—4 plants 12_{II}. [1966]

U. St Louis Co, NW corner Rosalie Tilles Pk, Ladue, *MacBryde 16:* **2n = 24**(2)—2 plants 12_{II}. [1966]

V. St Louis, 7113 Arsenal St, *MacBryde 27:* **2n = 30**(1)—1 plant 15_{II}. [1966]

W. St Louis, Missouri Bot Gard. *Suda 17:* **2n = 30**(5), **31**(1), **32**(2), **33**(1), **34**(1)—1 plant $14_{II}+2_{I}$, 4 plants 15_{II}, 1 plant $15_{II}+1_{I}$, 2 plants 16_{II}, 1 plant $15_{II}+3_{I}$, 1 plant $16_{II}+2_{I}$. [1967]

X. St Louis Co, 0.1 mi NE of Barrett Sta Rd on Dougherty Ferry Rd, *MacBryde 19:* **2n = 30** (1)—1 plant 15_{II}. [1966]

Y. St Louis Co, 1.1 mi W of Geyer Rd on W Adams Ave, Kirkwood, *MacBryde 5:* **2n = 29**(1)—1 plant $14_{II}+1_{I}$. [1966]

Z. St Louis Co, 326 E. Jefferson Ave, Kirkwood, *MacBryde 20:* **2n = 24**(1)—1 plant 12_{II}. [1966]

AA. St Louis, 0.4 mi N of Pkwy Lane on River Des Peres Pkwy, *MacBryde 25:* **2n = 30**(4), **31**(4), **32**(4), **34**(1), **34-36**(1, aneusomatic)—4 plants 15_{II}, 3 plants $15_{II}+1_{I}$, 1 plant $15_{II}+1_{I}$ & $14_{II}+1_{III}$, 1 plant $15_{II}+2_{I}$, 3 plants 16_{II}, 1 plant 17_{II}, 1 aneuso-

matic plant $14_{II}+1_{IV}+1_{III}+1_{I}$, $15_{II}+1_{IV}+2_{I}$, $15_{II}+1_{III}+2_{I}$, $15_{II}+1_{III}+1_{I}$(+1 fragment), $16_{II}+2_{I}$(+1 fragment), $16_{II}+3_{I}$, $16_{II}+3_{I}$(+1 fragment), $16_{II}+1_{III}+1_{I}$ (minimum of one cell each). [1966, 1967]

BB. St Louis, River Des Peres Pkwy, 0.3 mi NW of Gravois Ave, *MacBryde 26:* **2n = 31**(2)—2 plants $15_{II}+1_{I}$. [1966]

As summarized geographically in Fig. 1, the chromosome numbers of *C. virginica* (with frequency in parenthesis) are $2n = 22(9)$, 23(6), 24(49), 25(8), 26(9), 27(1), 29(4), 30(46), 31(18), 32(12), 33(3), 34(3), 35(1), 36(2), and 37(2). The significant features of these data include: (1) by far the most common numbers found in this random sample are $2n = 24$ and 30 with the majority of populations consisting of plants having chromosome numbers around either 24 or 30; (2) no distributional separation of cytotypes was noted, though only two populations (C, R) had plants of both major cytotypes based on maximum bivalent pairing; (3) except for univalent "formation" meiotic abnormality was infrequent (4) all plants examined were autopolyploids (cf. Lewis et al., 1967); and (5) frequency of polyploids does not represent a Gaussian curve, but rather a bimodal one with few plants having $2n = 27$ and 29 and none with $2n = 28$ (Fig. 2).

If univalents are eliminated in a consideration of chromosome number and only maximum bivalent pairing is used as a basis of number, then the frequency of those plants having 12_{II} and 15_{II} is greatly increased and the bimodal chromosomal curve is accentuated. This procedure is logical for the majority of plants with univalents were simply those having an unpaired chromosome; otherwise they usually exhibited normal meiosis. The univalent may or may not be associated with the haploid complement following meiosis, for often it was excluded during the process, or, if retained, then typically found in only one-half of the haploid nuclei. Based, therefore, only on bivalent formation, those having 12_{II} at metaphase I total 38.1% of the plants studied, those with 15_{II} total 35.3% or together about ¾ of all plants examined in the area. Of the remainder we found 11_{II} for 10% of the plants, 13_{II} for 3%, 14_{II} for 3%, 16_{II} for 8%, 17_{II} for 3% and 18_{II} for <1% as shown graphically in Fig. 2.

Of the 15 polyploid races found in the St. Louis area clearly those with $2n = 24$ and 30, and more particularly plants with 12_{II} and 15_{II}, are in the majority. The cytotype with $n = 12$ is also the most widespread autotetraploid for *C. virginica* as a whole and is probably an old tetraploid race derived early from the diploid $n = 6$ which is now limited to the relict area of the southern Appalachians (Lewis et al., 1967). Although of much less frequency plants with 11_{II} (usually $2n = 22$ and 23) total 10% of those studied; they are often found with plants having 12_{II} and probably represent those derived by chromosomal loss from the latter. Considered together plants with 11_{II} and 12_{II} account for about ½ of those examined, which emphasizes the significance of the $x = 6$ line at the tetraploid level in the St. Louis area.

Although plants with 15_{II} (usually $2n = 30$ and 31) are known elsewhere within the ranges of the primary tetraploid line ($x = 6, 7, 8$), their frequency does not appear to be nearly as great as that found in the St. Louis area (35%). This situation may be due to limited mass sampling elsewhere rather than to a unique-

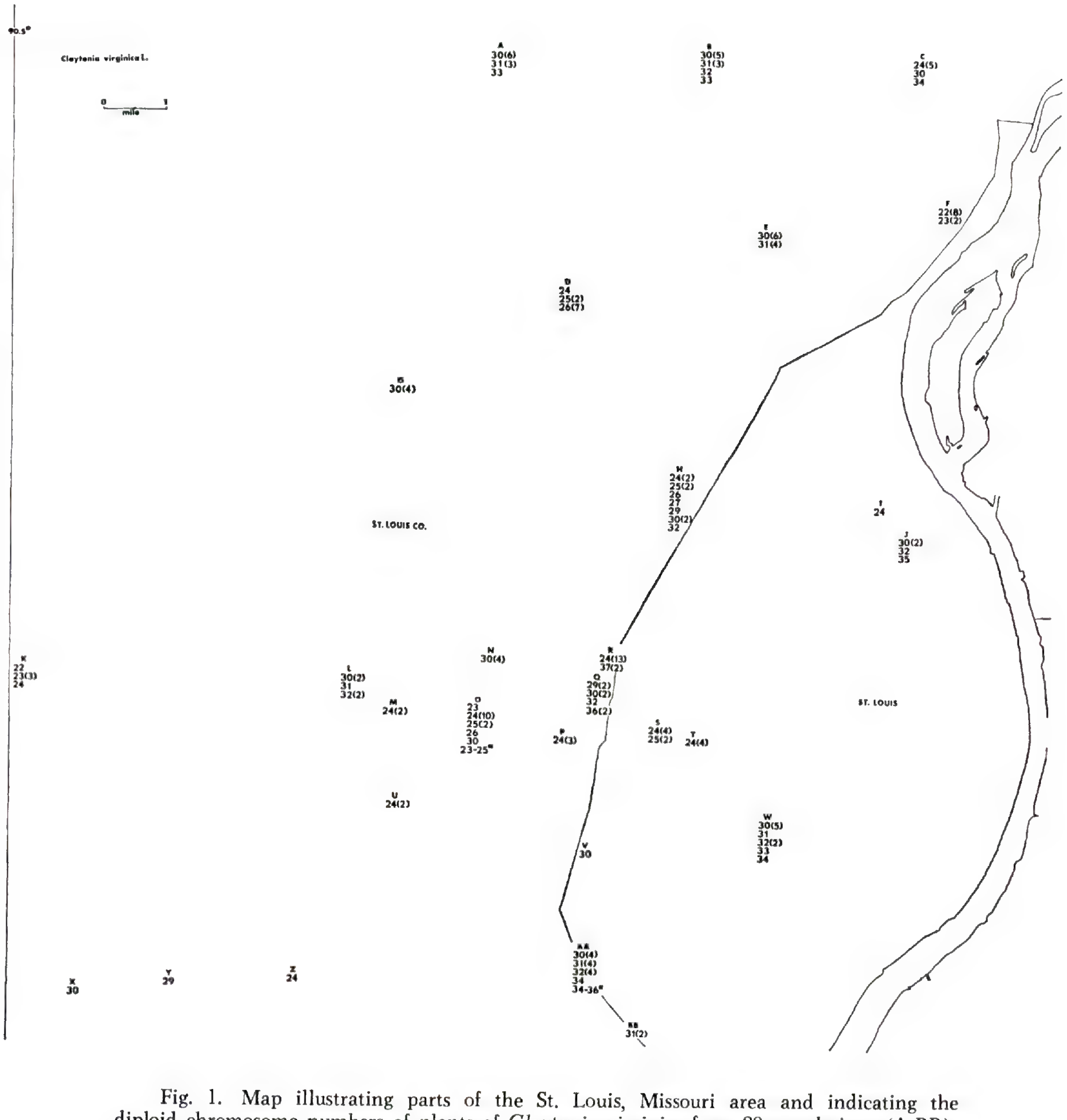

Fig. 1. Map illustrating parts of the St. Louis, Missouri area and indicating the diploid chromosome numbers of plants of *Claytonia virginica* from 28 populations (A-BB). The position of letters gives the exact locality of each population. Frequency of plants with particular chromosome numbers is given in parenthesis when more than one.

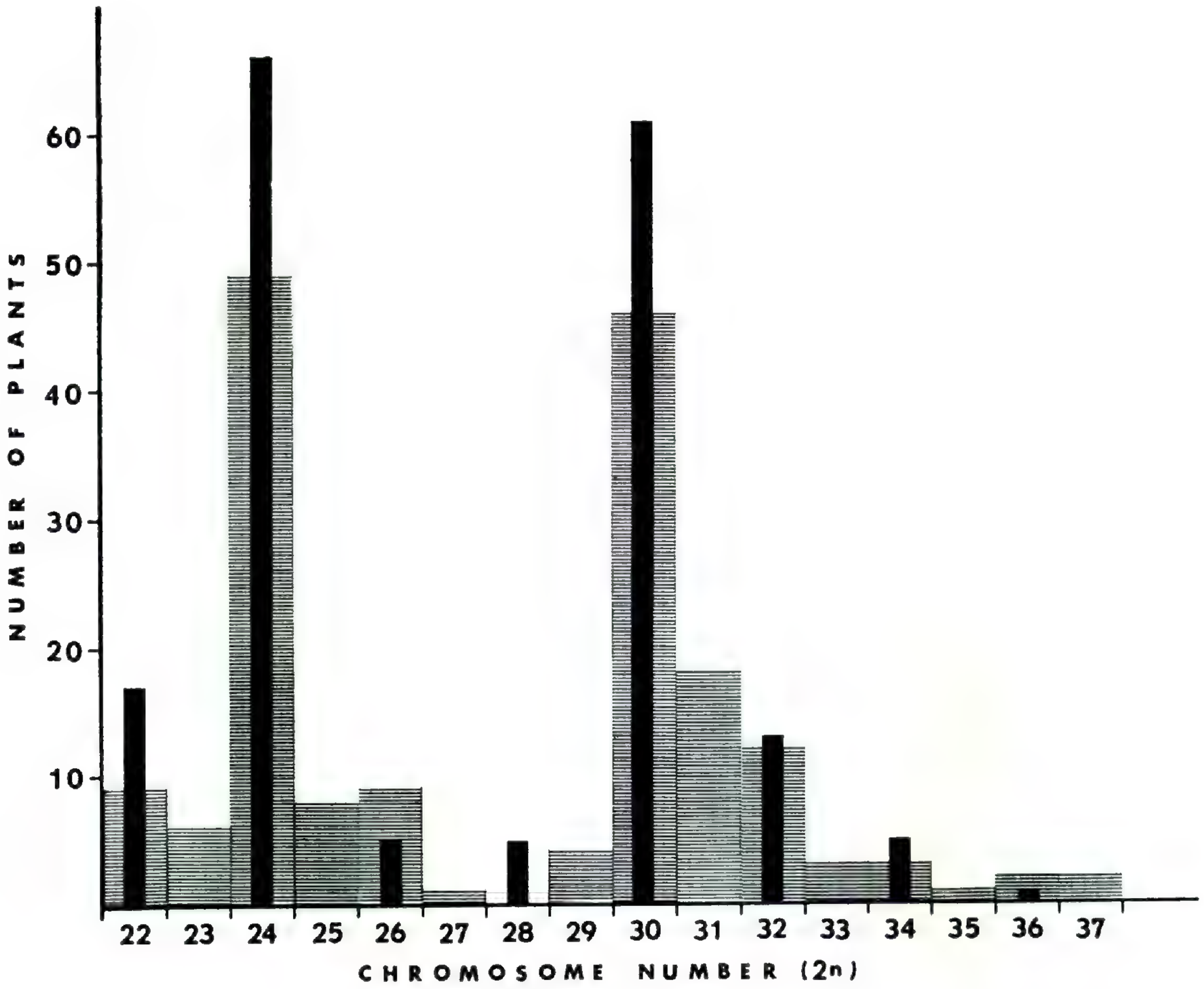

Fig. 2. Graphic representation of chromosome numbers for 173 plants of *Claytonia virgininica* examined from the St. Louis area. The wider bars indicate frequency of the total diploid chromosome number of plants, the narrower bars (solid) indicate frequency only of maximum bivalent formation converted to diploid chromosome number.

ness of plants from our area. Nevertheless a probable origin of a dominant secondary tetraploid needs exploration even if its success is of local significance only.

It may be merely coincidental that the $n = 15$ race is a multiple of the $x = 6$ line (as $5x$) or could it be possible that this seeming coincidence is related to a propensity of *C. virginica* to stabilize redundant chromosomes in multiples of six? An origin from $n = 12(4x) \times 18(6x)$ would give the necessary number of chromosomes, but the latter parent is at present very rare in the St. Louis area and in our sample no plant exhibited exclusively 18_{II} pairing. There is an alternative explanation which appears more plausible with available data. Plants with $2n = 30$, 31, and 32 are usually found together; moreover, throughout the Midwest the $2n = 32$ race is by far the most frequent (Lewis et al., 1967). Thus an origin by chromosomal loss from plants with $2n = 32$ is indicated, although, excepting the suggestion noted above, we find no reason for the high chromosomal frequency and apparent stabilization of the $2n = 30$ race in the St. Louis region.

Since most populations separated chromosomally into two groups, viz. with $2n = (22\text{-})24\text{-}(27)$ and $2n = (29\text{-})30\text{-}(37)$, plants in these groups were studied

for possible gross morphological differences. One distinct difference was found in leaf width: those plants with $2n = 24(\pm)$ have a maximum width of $\bar{\times} = 2.5(\pm 0.2)$ mm, those with $2n = 30(\pm)$ have much wider leaves with $\bar{\times} = 4.9(\pm 0.3)$ mm. Four populations with plants known to have chromosome numbers of both groups proved to be intermediate in both range and grand mean width of leaves (Table 1). These plants were largely with $2n = 24(\pm)$ and the grand mean of 2.7 mm, which is much narrower than mid-point, reflects the greater proportion of lower polyploids present in the mixed populations.

Table 1. Leaf width of plants of *Claytonia virginica* grouped by populational chromosome number.

Chromosome no.($2n$)	Leaf width (mm)[a]		No. of plants	No. of populations
	$\bar{\times}(s_{\bar{x}})$	$\bar{\times}$ range		
24[b]	2.5($\pm$0.2)	1.6-3.9	58	10
23-37	2.7($\pm$0.3)	2.1-3.6	22	4
30[b]	4.9($\pm$0.3)	3.0-6.9	83	13

[a] Calculated by populational mean of maximum leaf width per plant and reported as grand mean with standard error and mean range.

[b] Predominant chromosome number of populations.

Higher polyploids, therefore, can be separated morphologically from lower polyploids in the St. Louis area on the basis of leaf width. By their narrower leaves the lower polyploids ($n = 11$-13) are similar to those found elsewhere as well as to the diploid cytotypes based on 6 and 7. On the other hand the higher polyploids ($n = 15+$) from the St. Louis area resemble the same races in other regions and these are indistinguishable by leaf width from the diploid cytotype based on 8 (Lewis et al., 1967). No other gross morphological character correlated with leaf width or chromosome number.

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CYTOGEOGRAPHY OF CLAYTONIA VIRGINICA AND ITS ALLIES

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ABSTRACT

On the basis of chromosome numbers from more than 1,000 individuals of *Claytonia virginica* L. (*Portulacaceae*) throughout its range, a complex evolution of major cytotypes is discussed in relation to distribution and morphology. Chromosomal diversity is thought to have evolved from a base of $n = 6$ by hyperaneuploidy to $n = 7$ and 8 with each race giving rise to widespread and dominant primary tetraploids ($n = 12, 14, 16$). These in turn, and largely by hypoaneuploidy, formed many secondary tetraploid races, the most significant of which are $n = 11$ and 15. Higher polyploids from $6x$ to $12x$ where $x = 6$, and $6x$ and $8x$ where $x = 7$ are also discussed. Infraspecific phylogeny is compared with data for two allied species, *C. caroliniana* Michx. and *C. lanceolata* Pursh, which show striking parallels with *C. virginica* in chromosomal evolution. By one morphological character, leaf width, the cytotypes separate into two groups, not along diploid vs. polypoid lines, but rather a narrow-leafed var. *acutiflora* DC. with $n = 6, 7, 12\pm$, and $14\pm$ and a broad-leafed var. *virginica* with $n = 8$ and $16\pm$.

From collections made throughout eastern North America over 1,000 plants of *Claytonia virginica* L. (*Portulacaceae*) have been examined chromosomally. With the exception of Rothwell (1959) earlier studies have been limited in scope although all have made a substantial contribution to a cytogeographic understanding of the species (Bell, 1965; Davis & Bowmer, 1966; Lewis, 1959, 1962, 1967; Lewis et al., 1962, 1967; Rothwell & Kump, 1965). While these studies illustrated a wide diversity of chromosome number for *C. virginica* ($2n = 12$ to ca 191) none was extensive enough to indicate total distribution of all major cytotypes; rather only for a few from very limited areas, viz. dominance of $x = 7$ in eastern Texas (Lewis, 1962), $x = 8$ in Indiana (Rothwell, 1959), and $n = 12$ and 15 in the St. Louis, Missouri area (Lewis et al., 1967). We shall attempt with our additional data to present the distribution of cytotypes occuring in the eastern half of the continent and to suggest their probable evolution. Cytogeography and evolution of *C. virginica* will be compared with several allied species as well as briefly with the primitive species of *Claytonia*. In addition gross morphological diversity will be correlated with the various cytotypes and discussed in relation to distribution.

Cytological procedures followed those of Lewis (1962) and voucher specimens for each population were collected and are housed in the Missouri Botanical Garden herbarium (MO).

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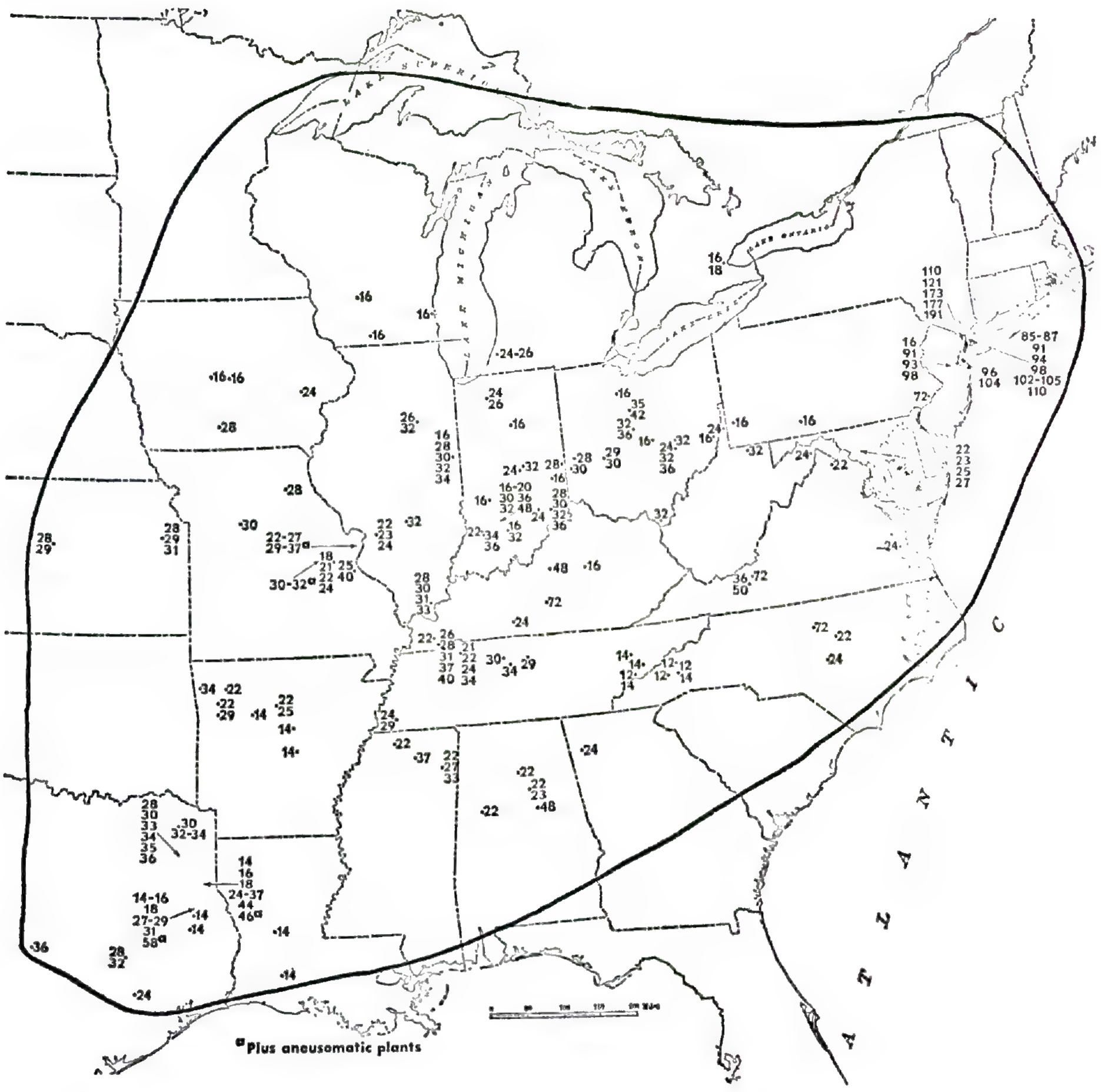

Fig. 1. Approximate distribution of *Claytonia virginica* in the eastern United States and adjacent Canada with known diploid ($2n$) chromosome numbers. Each dot or arrowhead represents the locality of a population or population area studied.

RESULTS AND DISCUSSION

Below are listed the chromosome numbers found for varying numbers of plants sampled at random from numerous populations. The exact locality of each population, arranged alphabetically by state and province, is noted together with the diploid number (frequency in parenthesis) and the meiotic configurations from PMC analysis generally at metaphase I or more rarely at anaphase I or metaphase II. Occasionally a count is based on somatic divisions either from root tips or floral buds. In addition earlier chromosomal reports for *C. virginica* are incorporated in the list and all are summarized by locality as diploid numbers in Fig. 1.

ALABAMA

Blount Co, 5.7 mi NW of Oneonta, *Lewis 6523:* **2n = 22**(4)—3 plants 11_{II}, 1 plant 11_{II} (+0−2 fragments).

St Clair Co, 1 mi NW of jct of Hwys 231 & 35, *Lewis 6524:* **2n = 22**(2), **23**(1)—2 plants 11_{II}, 1 plant $11_{II}+1_{I}$.

Talladega Co, Sycamore, *Lewis 6525:* **2n = 48**(5)—3 plants 24_{II}, 2 plants 24_{II}(+1 fragment).

Tuscaloosa Co, Tuscaloosa: **2n = 22**(2)—Rothwell (1959).

ARKANSAS

Faulkner Co, N Cadron Creek, 17.5 mi N of Conway, *Suda 8:* **2n = 14**(4)—4 plants 17_{II}.

Franklin Co, 13.6 mi S of Franklin-Madison Co line, *Oliver 466:* **2n = 29**(1)—1 plant $14_{II}+1_{I}$.

Madison Co, 9.3 mi SE of Madison-Washington Co line, *Oliver 468:* **2n = 22**(2)—2 plants 11_{II}.

Pope Co, 2.5 mi SE of Atkins, *Oliver 464:* **2n = 14**(4)—4 plants 7_{II}.

Pulaski Co, Burns Pk, Little Rock, *Suda 7:* **2n = 14**(11)—10 plants 7_{II}, 1 plant $6_{II}+2_{I}$ & 7_{II}.

Van Buren Co, 0.8 mi W of Bee Branch & jct of Hwys 92 and 65, *Oliver 463:* **2n = 22**(1), **25**(1)—1 plant 11_{II}, 1 plant $12_{II}+1_{I}$.

Washington Co, 0.1 mi NW of jct of Hwys 62 & 59, *Oliver 469:* **2n = 34**(1)—1 plant 17_{II}.

GEORGIA

Floyd Co, Rome, *Davis 6001* (as *C. bodinii* Holz.): ***n* = 12**(1)—Davis & Bowmer (1966).

ILLINOIS

Fayette Co: **2n = 32**(mc*)—Rothwell (1959).

Livingston Co, Rooks Creek, 4 mi W of Pontiac, *Lewis 6805:* **2n = 26**(1), **32**(1)—1 plant $11_{II}+4_{I}$.

Madison Co, 0.8 mi SW of Pocahontas, *Oliver 470:* **2n = 22**(2), **23**(1), **24**(1)—2 plants 11_{II}, 1 plant $11_{II}+1_{I}$, 1 plant 12_{II}.

Pope Co, 1.2 mi S of Renshaw, *Lewis 6596:* **2n = 28**(1), **30**(1), **31**(1) **33**(1)—1 plant 14+14, 1 plant 15_{II}, 1 plant $15_{II}+1_{I}$, 1 plant $16_{II}+1_{I}$.

Vermilion Co, *Bell 1441:* **n = 8, 14, 15, 16, 17**—Bell (1965).

INDIANA

Daviess Co, Westphalia: **2n = 22**(15)—Rothwell (1959); 1 mi S of Westphalia: **2n = 34, 36**(mc)—Rothwell (1959).

Fayette Co: **2n = 16**(mc)—Rothwell (1959).

Hancock Co.: 2 mi W. of Gem, *Lewis 6687:* **2n = ca 32**(1)—1 plant ca $14_{II}+4_{I}$.

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* Mass collection of buds, number of plants studied unknown.

Jennings Co, N Vernon: **2n = 24**(4)—Rothwell (1959).

Lawrence Co: **2n = 16, 32**(mc)—Rothwell (1959).

Marion Co, N city limits of Acton, *Oliver 474:* **2n = 24**(1)—1 plant 12_{II}.

Miami Co: **2n = 16**(mc)—Rothwell (1959).

Monroe Co, Beech Flats: **2n = 30**(5), **32**(5), **36**(3), **48**(1)—Rothwell (1959); id., Indiana Univ Campus: **2n = 16**(73), **17**(5), **18**(13), **19**(1), **20**(3), **30**(1), **32**(1)—Rothwell (1959).

Owen Co: **2n = 16**(mc)—Rothwell (1959).

Ripley Co, Versailles: **2n = 28**(1), **30**(2), **32**(2), **ca 36**(1)—Rothwell (1959).

Starke Co, San Pierre: **2n = 24** (1), **26**(1)—Rothwell (1959).

Wayne Co, 1 mi W of Centerville, *Oliver 475:* **2n = 28**(2)— 2 plants 14_{II}.

IOWA

Boone Co: **2n = 16**(mc)—Rothwell (1959).

Clarke Co, ca 2 mi S of Osceloa, *Lewis 6623:* **2n = ca 28**(1)—1 plant ca 14_{II}.

Johnson Co: **2n = 24**(mc)—Rothwell (1959).

Story Co: **2n = 16**(mc)—Rothwell (1959).

KANSAS

Douglas Co, Baldwin woods, SW of Vinland, *Lewis 6614:* **2n = 28**(2), **29**(2), **31**(2)—2 plants 14_{II}, 2 plants $14_{II}+1_{I}$, 2 plants $15_{II}+1_{I}$.

Ellsworth Co, ca 0.5 mi SW of Ellsworth-Salina Co line & Hwy 40, *Lewis 6615:* **2n = 28**(1), **29**(3)—1 plant 14_{II}, 2 plants $14_{II}+1_{I}$ & 14+15, 1 plant $14_{II}+1_{I}$ & $12_{II}+1_{III}+2_{I}$.

KENTUCKY

Calloway Co, 8.7 mi SE of Murray, *Lewis 6593:* **2n = 22**(1)—1 plant 11_{II}; id., 0.2 mi S of Hwys 641 and 464, *Lewis 6594:* **2n = 26**(1), **28**(1), **31**(1), **37**(1) (Lewis, 1967), **40**(1)—1 plant $12_{II}+2_{I}$(+0−1 fragment), 1 plant $12_{II}+4_{I}$ & $13_{II}+2_{I}$, 1 plant $15_{II}+1_{I}$ & two weeks later $13_{II}+5_{I}$, 1 plant $17_{II}+6_{I}$(+2−3 fragments).

Green Co, 1.4 mi NW of Greensburg, *Lewis 5603:* **n = 36**(2)—Lewis et al. (1962).

Jessamine Co: **2n = 16**(mc)—Rothwell (1959).

Nelson Co, Nazareth, *Lewis 6637:* **2n = 48**(1)—1 plant 24_{II}.

Warren Co, 0.7 mi NW of Petros, *Lewis 5606:* **n = 12**(2)—Lewis et al. (1962).

LOUISIANA

Acadia Par, 5.5 mi NNW of Iota, *Lewis 6600:* **2n = 14**(3)— 3 plants 7_{II}.

Rapides Par, 1 mi S of Hatwells, *Lewis 6602:* **2n = 14**(3)— 3 plants 7_{II}.

MARYLAND

Montgomery Co, 15 mi N of Washington, *Lewis 6633:* **2n = 22**(2), **23**(1) (Lewis, 1967), **25**(1), **27**(1)—2 plants 11_{II}, 1 plant $11_{II}+1_{I}$, 1plant $12_{II}+1_{I}$, 1 plant $12_{II}+3_{I}$.

MICHIGAN

Berrien Co, 10.3 mi NE of Three Oaks, *Oliver 484:* **2n = 24**(1), **25**(1), **26**(1)—1 plant 12_{II}, 1 plant $12_{II}+1_{I}$, 1 plant 13+13.

MISSISSIPPI

Itawamba Co, 6 mi W of Fulton, *Lewis 6501:* **2n = 22**(1), **27**(1), **33**(1)—1 plant 11_{II}, 1 plant $13_{II}+1_{I}$, 1 plant $16_{II}+1_{I}$.

Marshall Co, ca 1 mi SE of Holly Springs, *Lewis 6499:* **2n = 22**(4)—4 plants 11_{II}.

Union Co, 4.7 mi NW of Tallachatchie River by Hwy 78, *Lewis 6500:* **2n = 37**(1)—1 plant $18_{II}+1_{I}$.

MISSOURI

Franklin Co, Gray Summit, *MacBryde 6:* **2n = 31**(1)—1 plant $15_{II}+1_{I}$; id., *MacBryde 7:* **2n = 30-31**(1)—1 plant 15_{II} & $15_{II}+1_{I}$ (aneusomatic); id., *MacBryde 8:* **2n = 30**(1)—1 plant 15_{II}; id., **2n = 30**(1), **32**(3)—Rothwell (1959); St Clair, village of Parkway, *MacBryde 1:* **2n = 18**(1), **21**(1), **22**(2)—1 plant $8_{II}+2_{I}$, 1 plant $10_{II}+1_{I}$ (+0−1 fragment), 1 plant $9_{II}+4_{I}$ & 11+11, 1 plant $9_{II}+1_{III}+1_{I}$ (rare), $10_{II}+2_{I}$(few) & 11_{II} [1966]; id., *Suda 18:* **2n = 22**(3), **24**(1), **26**(1)—1 plant $10_{II}+2_{I}$, 2 plants 11_{II}, 1 plant 12_{II}, 1 plant 13_{II} [1967]; St Clair High School, *MacBryde 2:* **2n = 22**(3)—3 plants 11_{II} [1966]; id., *MacBryde 3:* **2n = 24**(2)—2 plants 12_{II}.

Jefferson Co, vic of Rice Lodge, *Lewis 6603:* **2n = 25**(1), **40**(1)—1 plant $12_{II}+1_{I}$, 1 plant $18_{II}+4_{I}$(+0−1 fragment).

St Louis & St Louis Co: **2n = 22**(9), **23**(6), **24**(49), **25**(8), **26**(9), **27**(1), **29**(4), **30**(46), **31**(18), **32**(12), **33**(3), **34**(3), **35**(1), **36**(2), **37**(2)—Lewis, Suda & MacBryde (1967); id., Barque Creek; **2n = 32**(1), **34**(1)—Rothwell (1959); id., Clay City: **2n = 22**(mc)—Rothwell (1959).

Saline Co, Blackwater River, 1.3 mi S of Hwys 40 & YY, *Lewis 6611:* **2n = ca 30**(1)—1 plant ca 15_{II}.

Shelby Co, Salt River at Hwy 36, *Lewis 6627:* **2n = 28**(1)— 1 plant 14_{II}.

NEW YORK

Bronx, Bronx Pk: **2n = 91**(1), **98**(1), **103**(1), **105**(1); id., Pelham Bay Pk: **2n = 85**(1), **86**(1), **87**(1); id., Van Cortlandt Pk: **2n = 94**(1), **102**(1), **104**(1), **110**(1)—Rothwell & Kump (1965).

Staten I, Latourette Pk: **2n = ca 96**(1); Willowbrook Pk: **2n = 104**(1)—Rothwell & Kump (1965).

NEW JERSEY

Bergen Co, Palisades Interstate Pk: **2n = 110**(1), **121**(1), **173**(1), **177**(1), **ca 191**(1)—Rothwell & Kump (1965).

Somerset Co, East Millstone, **2n = 93**(1)—Rothwell & Kump (1965); id., Martinsville: **2n = 98**(1)—Rothwell & Kump (1965); id., Pluckemin: **2n = 16**(23), **91**(1), **93**(1)—Rothwell & Kump (1965).

NORTH CAROLINA

Buncombe Co: **2n = 12**(2), **14**(1)—Rothwell (1959); id., 0.2 mi W of Swannanoa, *Lewis 6582:* **2n = 12**(2)—2 plants 6_{II}.

Harnett Co: **2n = 24**(mc)—Rothwell (1959).

Haywood Co, 2 mi E of Maggie Post Office, *Lewis 6581:* **2n = 12**(5)—5 plants 6_{II}; id., *Lewis 6662:* **2n = 12**(2)—2 plants 6_{II}.

Orange Co: **2n = 72**(2)—Rothwell (1959).

Wake Co, Raleigh: **2n = 22**(3)—Rothwell (1959).

OHIO

Belmont Co, 4.2 mi E of Hwy 149 by Hwy 70, *Lewis 6682:* **2n = 16**(4)—4 plants 8_{II}.

Clark Co, 1.2 mi E of Harmony, *Lewis 6685:* **2n = 29**(1), **30**(1)—1 plant $13_{II}+3_{I}$ & $14_{II}+1_{I}$, 1 plant 15_{II}.

Crawford Co, 1.7 mi S of Bucyrus, *Oliver 478:* **2n = 35**(3), **42**(1)—3 plants $17_{II}+1_{I}$, 1 plant $20_{II}+2_{I}$ & 21_{II}.

Delaware Co: Delaware-Franklin Co line & Hwy 23, *Oliver 477:* **2n = 32**(1), **36**(1)—1 plant 16_{II}, 1 plant 18_{II}.

Lawrence Co: **2n = 32**(mc)— Rothwell (1959).

Licking Co: 1.5 mi E of Hwy 79 by Hwy 70, *Lewis 6684:* **2n = 16**(4)—4 plants 8_{II}.

Montgomery Co, 1 mi E of Englewood, *Oliver 476:* **2n = 28**(1)—1 plant 14_{II}.

Muskingum Co, ca 2 mi W of Bridgeville, *Lewis 6683:* **2n = 32**(2)—2 plants 16_{II}; id., Zanesville, *Davis 6011:* **n = 12, 16, 18**—Davis & Bowmer (1966).

Preble Co, ca 2 mi W of Lewisberg, *Lewis 6686:* **2n = ca 30**(1)— 1 plant ca 15_{II}.

Seneca Co, 0.3 mi E of jct of Hwys 4 & 162, *Oliver 479:* **2n = 16**(1)—1 plant 8+8.

ONTARIO

Wentworth Co, Royal Bot Gard, Hamilton, *Lewis 6630:* **2n = 16**(1), **18**(1)—1 plant 8_{II}, 1 plant 9_{II}.

PENNSYLVANIA

Bedford Co, 1 mi W of Manns Choice, *Lewis 6680:* **2n = 16**(5)— 1 plant $7_{II}+2_{I}$, 4 plants 8_{II}.

Philadelphia Co, Philadelphia, *Davis 6007:* **n = 36**—Davis & Bowmer (1966).

Washington Co, 3.5 mi ENE of Claysville by Hwy 70, *Lewis 6681:* **2n = 16**(5)—5 plants 8_{II}.

TENNESSEE

Davidson Co, suburbs NE of Nashville by Hwy 41A, *Lewis 6591:* **2n = 30**(2)—2 plants $14_{II}+2_{I}$; id., 0.4 mi S of Hwy 40 on Old Hickory Rd, *Lewis 6645:* **2n = 34**(1)—1 plant 17_{II}, $16_{II}+2_{I}$ & $15_{II}+1_{III}$ & 1_{I}.

Knox Co, Tennessee River opposite Airport I, *Lewis 6646:* **2n = 14**(2)—2 plants 7_{II}.

Sevier Co, 0.4 mi E of Gatlinberg, *Lewis 6651:* **2n = 14**(2)—2 plants 7_{II}; id., N slope of Sugarbay Mt, *Lewis 6649:* **2n = 12**(2), **14**(3)—2 plants 6_{II}, 3 plants 7_{II}.

Shelby Co, 0.8 mi NW of Capleville, *Lewis 6496:* **2n = 24**(1), **29**(1)—1 plant 12_{II}, 1 plant $10_{II}+1_{III}+6_{I}$, $11_{II}+7_{I}$ & $12_{II}+5_{I}$.

Stewart Co, 2.8 mi E of Tennessee River by Hwy 79, *Lewis 6592:* **2n = 21**(1), **22**(3), **24**(2), **34**(1)—1 plant $10_{II}+1_{I}$, 3 plants 11_{II}, 2 plants 12_{II}, 1 plant $16_{II}+2_{I}$.

Wilson Co, Lebanon, *Lewis 6590:* **2n = 29**(1)—1 plant $12_{II}+5_{I}$ (+0−1 fragment).

TEXAS

Angelina Co, Lufkin: **2n = 14**(1)—Lewis (1959).

Burnet Co, 4-5 mi S of Bertram, *Lewis 6479:* **2n = 36**(6)—4 plants 18_{II} & 18+18, 2 plants 18_{II} & $17_{II}+2_{I}$.

Brazos Co, College Sta: **2n = 28**(1), **32**(1)—Rothwell (1959).

Nacogdoches Co, 12 mi S of Nacogdoches: **2n = 14**(1)—Lewis (1959); id., vic of Nacogdoches, *Lewis 5551A-C:* **2n = 14**(78), **15**(1), **16**(5), **18**(2), **27**(1), **28**(1), **29**(1), **31**(2), **58**(1)—Lewis (1959, 1962).

Panola Co, Carthage & vic, *Lewis 5560A-O:* **2n = 14**(37), **25**(1), **26**(1), **28**(18), **29**(18), **30**(5), **31**(3), **32**(3), **33**(1), **36**(2), & aneusomatics—Lewis (1962); id., *Lewis 5560E, F, J:* **2n = 14**(1), **28**(5), **29**(1), **30**(2), **32**(1), **35**(1)—4 plants 14_{II}, 1 plant $14_{II}+1_{I}$, 2 plants 15_{II}, 1 plant $13_{II}+6_{I}$ & $14_{II}+4_{I}$, 1 plant $13_{II}+1_{IV}+5_{I}$ & $14_{II}+7_{I}$ [1963]; id.,*Suda 1, 2, 2E, F, H-L:* **2n = 14**(24), **16**(1), **18**(2), **24**(8), **25**(2), **26**(6), **27**(3), **28**(52), **29**(18), **30**(11), **31**(1), **32**(4), **34**(1), **35**(3), **36**(1), **37**(2), **44**(1), **46**(1)—24 plants 7_{II} or 7+7, 1 plant 8_{II}, 2 plants 9_{II}, 8 plants 12_{II} or 12+12, 2 plants $12_{II}+1_{I}$, 6 plants 13_{II} or 13+13, 3 plants $13_{II}+1_{I}$, 3 plants $13_{II}+2_{I}$, 48 plants 14_{II} or 14+14, 1 plant 28_{I}, 1 plant $12_{II}+5_{I}$ & $13_{II}+3_{I}$, 2 plants $13_{II}+3_{I}$, 15 plants $14_{II}+1_{I}$, 1 plant $5_{II}+20_{I}$ & $10_{II}+10_{I}$, 1 plant $14_{II}+2_{I}$, 1 plant $14_{II}+2_{I}$ & 15_{II}, 8 plants 15_{II} or 15+15, 1 plant $15_{II}+1_{I}$, 1 plant $14_{II}+4_{I}$, 2 plants $15_{II}+2_{I}$, 1 plant 16_{II}, 1 plant $14_{II}+6_{I}$, 3 plants $14_{II}+7_{I}$, 1 plant $14_{II}+8_{I}$, 1 plant $15_{II}+7_{I}$, 1 plant $18_{II}+1_{I}$, 1 plant $20_{II}+4_{I}$, 1 plant $22_{II}+2_{I}$ & 23_{II}. [1967]

Titus Co, Mt Pleasant, *Suda 5:* **2n = 30**(4), **32**(1), **33**(1), **34**(1)—3 plants 15_{II}, 1 plant $13_{II}+1_{IV}$&15_{II}, 1 plant $15_{II}+2_{I}$&16_{II}, 1 plant $12_{II}+1_{VIII}+1_{I}$, 1 plant $12_{II}+1_{VIII}+2_{I}$.

Upshur Co, Gilmer, *Suda 4:* **2n = 28**(1), **30**(3), **33**(2), **34**(3), **35**(1), **36**(1)—1 plant 14_{II}, 1 plant $14_{II}+2_{I}$, 2 plants 15_{II}, 1 plant $12_{II}+1_{VIII}+1_{I}$, 1 plant $16_{II}+2_{I}$, 1 plant $13_{II}+1_{VIII}$, 1 plant $12_{II}+1_{VIII}+2_{I}$ & $16_{II}+2_{I}$, 1 plant 17_{II}, 1 plant $13_{II}+1_{VIII}+1_{I}$, 1 plant $15_{II}+1_{IV}+2_{I}$, $15_{II}+1_{VI}$, $16_{II}+1_{IV}$ & $17_{II}+2_{I}$.

Waller Co, Hempstead, *Davis 6000* (as *C. bodinii* Holz.): **n = 12**—Davis & Bowmer (1966).

VIRGINIA

Clark Co: 1.3 mi E of Shenandoah River by Hwy 50, *Lewis 6672:* **2n = 22**(7)—7 plants 11_{II}.

Montgomery Co, 3 mi SE of Blacksburg, *Lewis 6670:* **2n = ca 72**(2)—2 plants ca 36_{II}; id., McCoy, *Lewis 6671:* **2n = 36**(1), **50**(1)—1 plant $16_{II}+4_{I}$, $17_{II}+2_{I}$&18_{II}, 1 plant $21_{II}+1_{III}+5_{I}$ (+1 fragment).

James City Co, Williamsburg, *Davis 6005:* **n = 12**—Davis & Bowmer (1966).

WEST VIRGINIA

Hampshire Co, Ice Mt, 13 mi SE of Slavesville, *Lewis 6673:* **2n = 24**(6)—6 plants 12_{II}.

Monongalia Co, Morgantown, *Lewis 6678:* **2n = 32**(5)—5 plants 16_{II}.

Ohio Co, 1 mi W of W Va & Pa state line, *Davis 6010:* **n = 12**—Davis & Bowmer (1966).

WISCONSIN

Green Co: **2n = 16**(mc)—Rothwell (1959).

Milwaukee Co: **2n = 16**(mc)—Rothwell (1959).

Sank Co: **2n = 16**(mc)—Rothwell (1959).

Cytology

Before proceeding with a discussion of major cytotypes two phenomena will be noted briefly. These include aneusomaty, i.e. variation of chromosome number intra-individually, which was found by Lewis et al. (1967) in the St. Louis area and earlier in eastern Texas (Lewis, 1962). No additional data can be added to this phenomenon. We wish also to mention the results of Rothwell & Kump (1965) from the New York area in which they reported highly polyploid individuals ($2n$ = 85 to ca 191) occasionally associated with meiotically regular diploids ($2n$ = 16). Such individuals have not been found elsewhere, but their diversity in New York (perhaps formed in response to some local environmental circumstance, e.g. viruses) does illustrate a propensity for mass chromosomal duplication without apparent harm to the individual.

Elsewhere the results are more orderly. Of the three major diploid cytotypes (Fig. 2), that having n = 6 is restricted to the geologically old and well-known relict and refugial area in the southern Appalachian Mountains. Here, found in mixed and separate populations, are plants with n = 7. This race is also found in the geologically similar Ozarks and to the south of these mountains as a common weed almost to the Gulf of Mexico. The n = 7 race is now disjunct, but very probably had a common origin and was continuous much earlier. The third major diploid race is based on 8; it dominates the northern distribution of *C. virginica* and has by far the greatest continuous range of any diploid. To the south, its limits parallel somewhat the southern expansion of the last glaciation (Fig. 2). Rarely individuals with n = 8 occur outside this area, e.g. in eastern Texas, but they probably represent spontaneous, local aneuploids quite apart from the major trends of evolution.

Other diploid cytotypes are known, but these are rare and none has a distinct distribution. The n = 9 race, for example, is found very rarely in eastern Texas in populations dominated by plants with n = 7 and where n = 8 is rare in a declining frequency from n = 7-8-9 with only one plant having $2n$ = 15. Paralleling this Rothwell (1959) reported in a single population 73 plants with n = 8, 13 with n = 9, and 3 with n = 10 as well as aneuploids with $8_{II}+1_{I}$ and $9_{II}+1_{I}$. From only two plants of an Ontario population (*Lewis 6630*) we found one plant with n = 8 and one with n = 9. Although it cannot be excluded that a race dominated by plants having n = 9 may yet be found in the northern range of *C.*

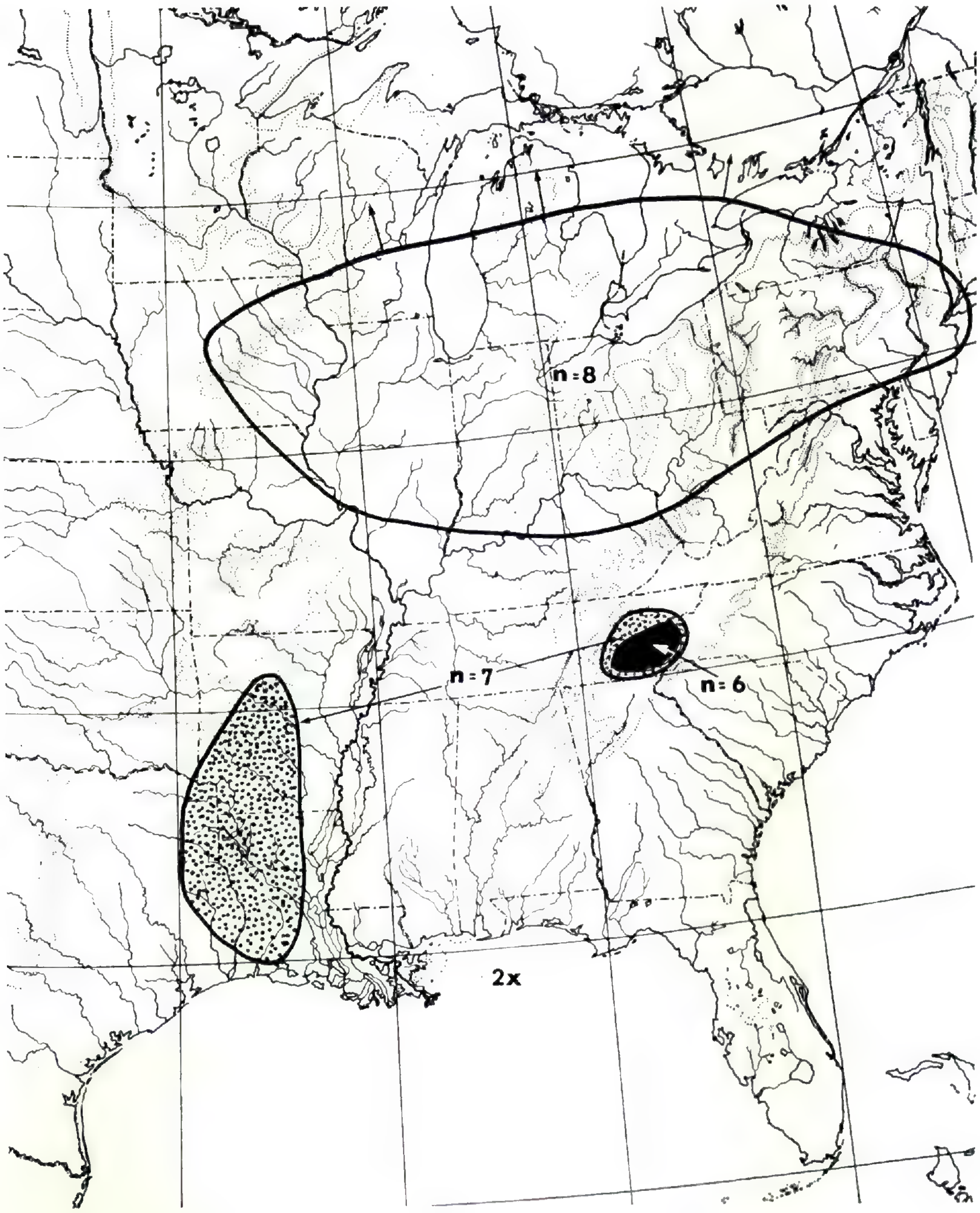

Fig. 2. Distribution of the major diploid cytotypes ($n = 6, 7, 8$) of *Claytonia virginica* in eastern North America.

virginica, where counts are as yet meagre, autodiploids other than $n = 6$, 7, and 8 are infrequent and sporadic and probably arose by chromosomal gain through meiotic nondisjunction over and over again locally from plants representing the dominant diploid for the area.

The primary tetraploid cytotypes of each of the major diploid races ($n = 12$, 14, 16) are very common and have widespread overlapping distributions (Fig. 3).

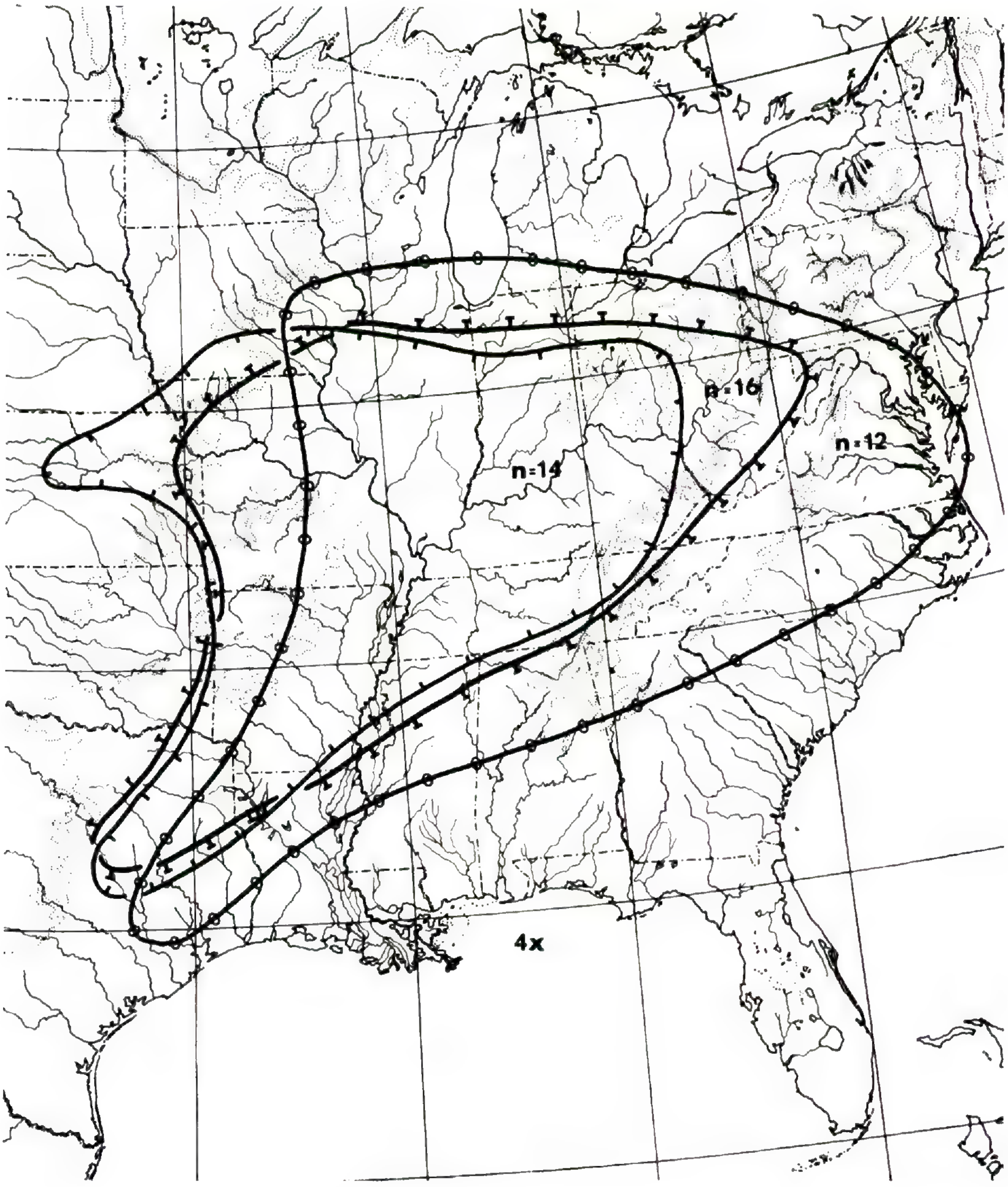

Fig. 3. Distribution of the major tetraploid cytotypes ($n = 12, 14, 16$) of *Claytonia virginica* in eastern North America.

All major tetraploids may be found together, but invariably one or two races dominate at any one locality. For example in the St. Louis area, where diploids are unknown, two tetraploid races are dominant and more or less of equal frequency; they usually are found at distinct localities even in this small area although both races are occasionally found together.

Secondary tetraploid races are also frequent, but usually in association with primary tetraploid cytotypes from which they probably arose. In the St. Louis area $n = 15$ is much more common than $n = 16$, but at several localities both occur

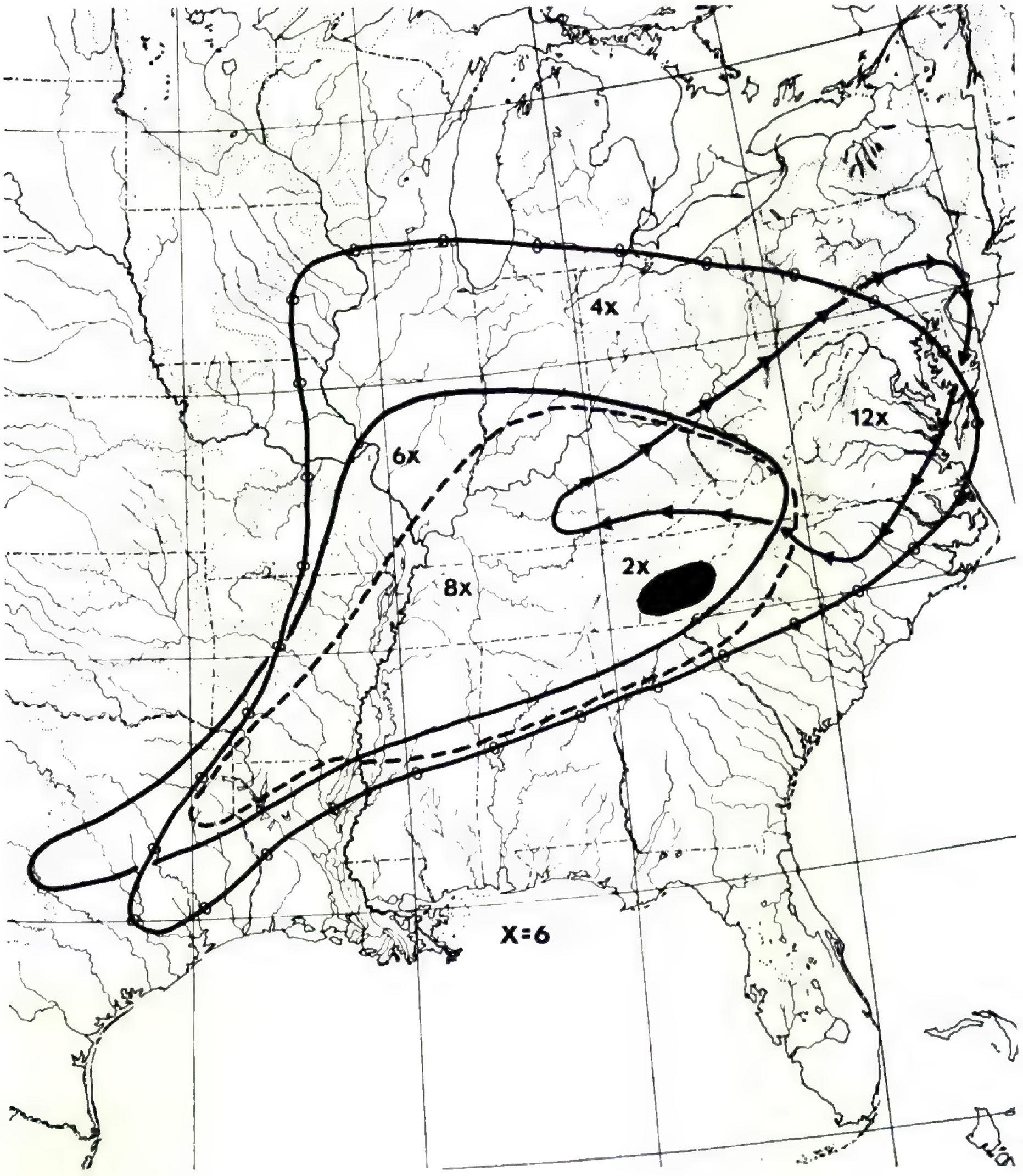

Fig. 4. Distribution of the $x = 6$ cytotypes of *Claytonia virginica* in eastern North America.

in addition to $15_{II}+1_{I}$. Elsewhere particularly in the Midwest this pattern is repeated or reversed, i.e. dominance of $n = 16$ with fewer secondary tetraploids (cf. Fig. 1). Widespread also are plants with $n = 11$; these are secondary tetraploids probably formed by hypoaneuploidy from those with $n = 12$ with which they are usually associated. Sporadically throughout the range of *C. virginica* other secondary tetraploids are found, but none is frequent.

Of the higher polyploid races only those with $n = 18$, presumably hexaploids in the $x = 6$ line, are frequent and widespread; less common are those with $n =$

24 (8*x*) and 36 (12*x*) based on 6. More infrequent still are those with $n = 21$ (6*x*) and 28 (8*x*) where $x = 7$.

To facilitate their study according to base number the major cytotypes with distributions are illustrated in Fig. 4-6. The $x = 6$ line has the greatest range and is the most highly polyploid (Fig. 4); as already noted the 2*x* is restricted to the southern Appalachians and the 4*x* is widely distributed; the 6*x* is less frequent but found within the range of the tetraploid; the 8*x* is rare though similar to the hexaploid in distribution; and the 12*x* is also rare but more restricted (mid-Atlantic states and mid-Appalachians).

For the $x = 7$ race (Fig. 5) we have noted the disjunct distribution of the southern 2*x* as well as the wide range of the 4*x* race. The occurrence of the 6*x* and 8*x* races are shown in Fig. 5; both are very rare and local.

Only two races are clearly based on 8. The diploid is northern, the tetraploid extends more to the south and both are of wide range (Fig. 6). No octoploid, $n = 32$, is known.

Comparative frequency for all significant cytotypes is presented in Fig. 7, a rough index at best because sampling has been better in some areas than in others. Yet the diagram does accurately reflect, we believe, an increase in frequency among the diploid races from $n = 6$ to 8 with an abrupt decrease to $n = 9$ and 10 (representatives of the latter race may have evolved by chromosomal loss from tetraploids or by hyperaneuploidy from diploids). This sequence suggests hyperaneuploidy from $n = 6$, a very old and apparently relict race for *C. virginica* and one which may be basic for the genus if not the family (see below). Perhaps also the antiquity of this basic number is reflected by the extensive polyploid series from $n = 6$, far greater than for any other basic line.

Judging from Fig. 7, however, *C. virginica* is dominated by plants at the tetraploid level. They presumably evolved along at least three distinct lines from $n = 6$ to 12, $n = 7$ to 14, and $n = 8$ to 16, perhaps through unreduced gametes. The first successful mutation was probably from $n = 6$ to 12, the former now very restricted, the latter now forming one of the largest and most frequent cytotypes in the species. They are not known to be sympatric alhough our data are meagre from the mid-Appalachian region where they might occur together. Cytotypes of the other lines, however, are often found at the same locality, e.g. $n = 7$ and 14 in eastern Texas, $n = 8$ and 16 in Indiana.

A significant feature of tetraploids is the frequency of their secondary races, particularly $n = 11$ and 15 (Fig. 7). Their origins from $n = 12$ and 16, respectively, have already been noted. Other such tetraploids are known and these in total account for a large fraction of individuals examined. Clearly chromosomal change at the tetraploid level has been much greater than at the diploid level; presumably this redundancy of chromosomes has allowed a greater shift in complements without deleterious effects. Moreover change among tetraploids appears strongly downward (hypoaneutetraploidy) in contrast to the diploid level where chromosomal gain has apparently been more important (hyperaneudiploidy).

Probably through unreduced gametes or less likely by doubling of 2*x*-4*x* crosses (no definite triploid has yet been found) or by both, the higher polyploids

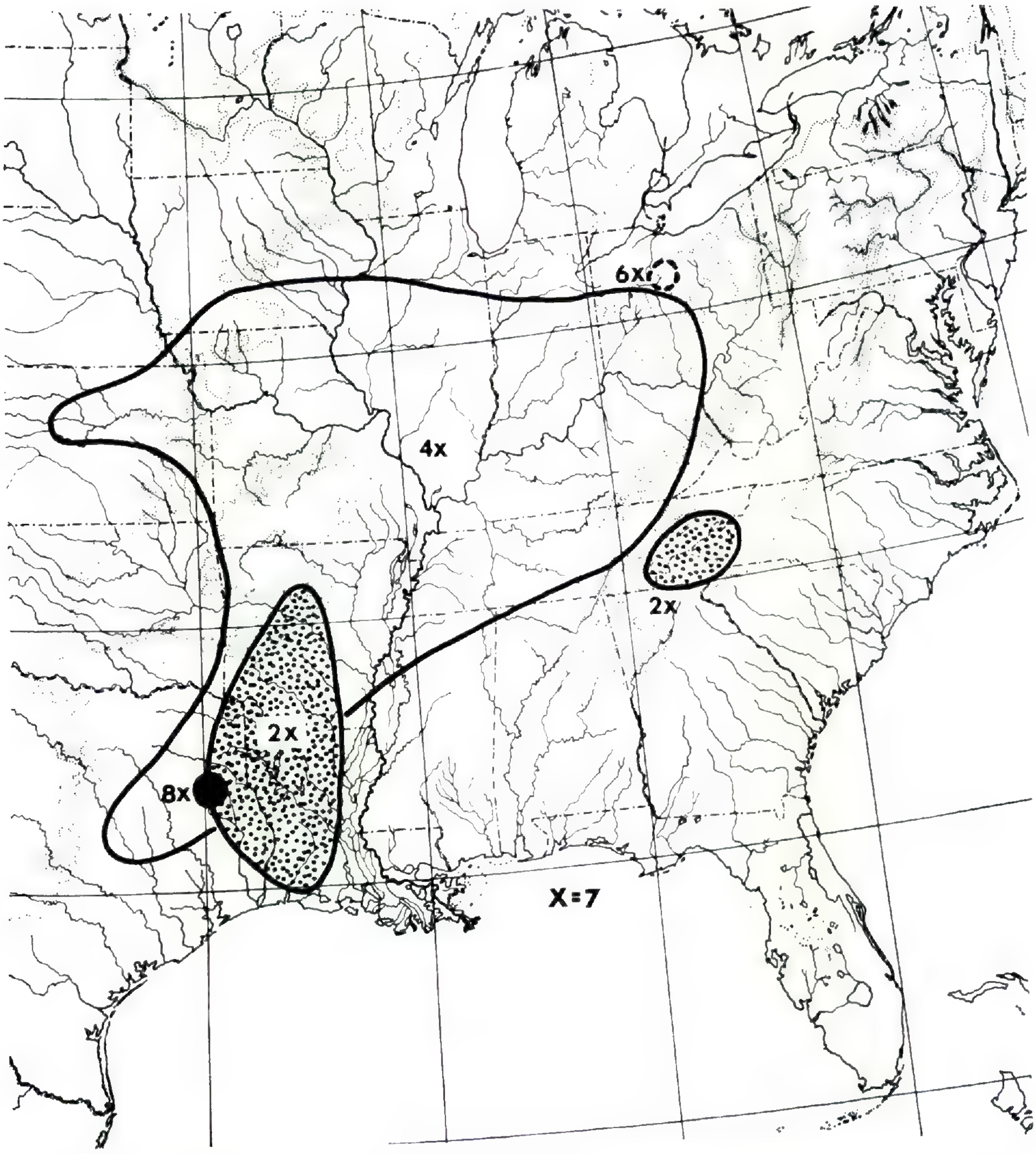

Fig. 5. Distribution of the $x = 7$ cytotypes of *Claytonia virginica* in eastern North America.

evolved. Their frequency and direction of evolution are suggested in Fig. 7.

After this scheme of infraspecific phylogeny for *C. virginica* had been organized, we decided to compare it with the chromosomal data available for several closely related species; fortunately, the best known cytologically in the genus were two allied corm-bearing species. These are *C. caroliniana* Michx. of the Appalachians and northern parts of eastern North America and *C. lanceolata* Pursh from the Rocky Mountains (cf. Lewis, 1967, Table 2).

Claytonia caroliniana consists of two dominant cytotypes, $n = 8$ and 12, with very few plants representing other races (Fig. 8). The $n = 12$ race is found in the southern Appalachians while the $n = 8$ race is known from northern West Virginia

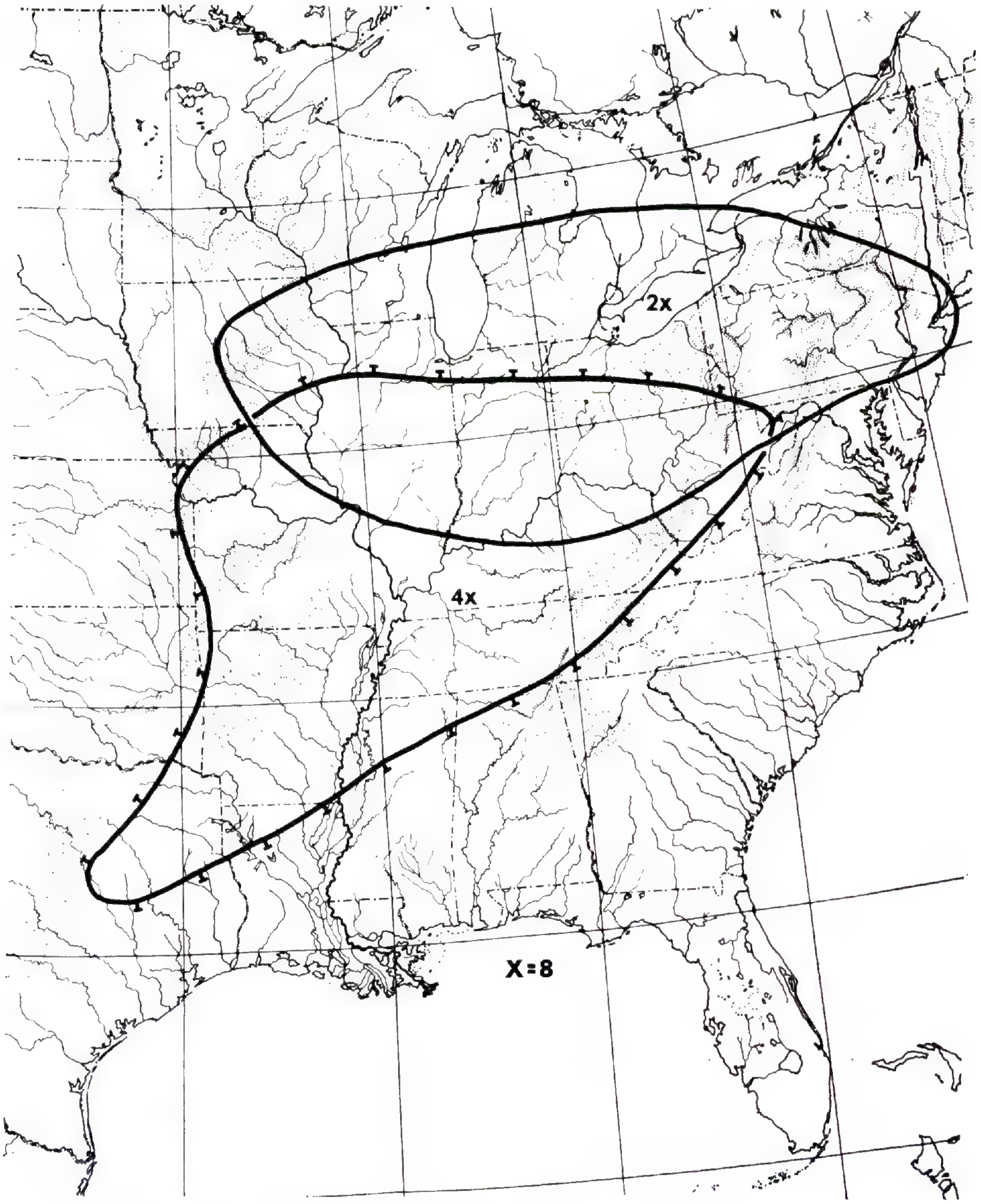

Fig. 6. Distribution of the $x = 8$ cytotypes of *Claytonia virginica* in eastern North America.

to Quebec. Heretofore these cytotypes with their distinct if not nearly disjunct distributions failed to have "meaning"—how could such races different by four pairs of chromosome evolve? However, superimposed on the scheme for *C. virginica* we find: (a) hyperaneudiploidy from $n = 6$ to 8; (b) loss of two diploid races ($n = 6$ and 7) both of which are of restricted frequency in *C. virginica;* (c) proliferation of the $n = 8$ race to the north, a characteristic feature of *C. virginica;* (d) before extinction of $n = 6$ the evolution of the tetraploid $n = 12$, a race well-

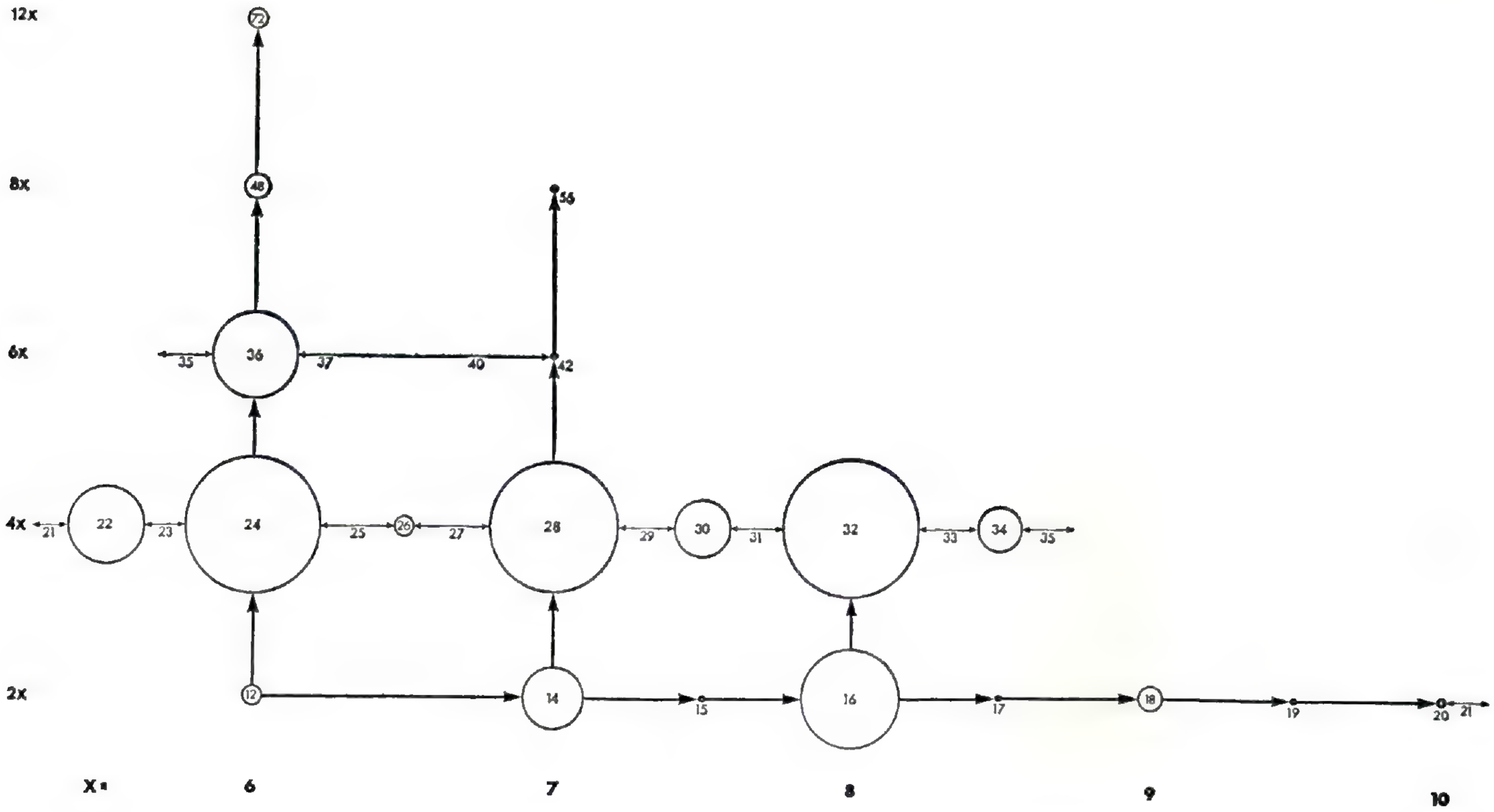

Fig. 7. Comparative frequency of cytotypes (as $2n$) in *Claytonia virginica* and suggested evolutionary direction. The smallest circle represents the occurrence of a race in one population, others to scale.

established also in *C. virginica;* and (e) evolution to a higher polyploid level based on 6, again a development typical of *C. virginica.* Such parallels are striking and they serve to strengthen the infraspecific scheme proposed for *C. virginica* where greater diversity tends to shroud conclusions.

Claytonia lanceolata also possesses a dominant race with $n = 8$ now known from Washington, Oregon, Idaho, Colorado, and Utah (cf. Lewis, 1967) as well as a widespread $n = 12$ race (Fig. 8). Particularly at the diploid level infraspecific evolution has been similar to *C. caroliniana;* at the polyploid level close to *C. virginica* where $x = 6$ ($4x$, $6x$, $8x$, $12x$).

Thus the only closely allied, widespread, corm-bearing species of *Claytonia* share a similar phylogeny, but how does this proposal for an advanced perennial group (Swanson, 1966) compare with the most primitive species in the genus? Swanson considers those perennials having taproots in the sect. *Caudicosa* (Gray) Von Poellnitz primitive; of these, two species are known chromosomally (definite counts only). *Claytonia sibirica* L. has three races, $n = 6$, 12, 18, based on numerous counts from many areas (Lewis, 1967). Three races are also reported for *C. megarhiza* (Gray) Parry ex S. Wats. from only three populations (or plants ?): var. *megarhiza* with $n = 16$ from Colorado (Davis & Bowmer, 1966) and $2n = 36$ from Alberta (Taylor & Brockman, 1966), and var. *bellidifolia* (Rydb.) C. L. Hitchc. from Oregon as $n = 12$ (Davis & Bowmer, 1966). It appears that *C. megarhiza* is yet another multibasic species, but having in common with *C. sibirica* both $n = 12$ and 18 which are $4x$ and $6x$ races based on 6. Therefore, the primitive

sect. *Caudicosa* has at least one predominant base number, $x = 6$, a number very probably basic for the genus, including the corm-bearing species.

The only other well-studied portulacaceous genus is *Talinum* where $x = 12$. In all probability this base is derived from $x = 6$ which may prove to be the prototypic number of the family.

Morphology

Variation in gross morphology of *C. virginica* is aptly summarized by Davis (1966) who noted that the narrow-leafed variety which he called *simsii*[2] "cannot be distinguished from var. *virginica* by shape, length, or texture of sepals, bracts, or petals, because there are all gradations and combinations of characters between the extremes. However, in the southern part of the range many of the plants tend to be smaller and have very narrow leaves." Even though the narrow-leafed variety is frequent in the southern range of the species the broad-leafed form is also known in the south (Alabama and Mississippi) while the narrow-leafed variety is abundant as far north as eastern Missouri (Lewis et al., 1967) and northern West Virginia (*Lewis* 6673) and Maryland (*Lewis* 6633). In what way, if at all, do these varieties correlate with the many cytotypes and their distributions?

From among the largely $2x$ and $4x$ cytotypes with $x = 7$ examined in eastern Texas, Lewis (1962) found only the narrow-leafed variety. There was no difference between diploids and tetraploids in leaf width or in any other character studied. However, from the St. Louis area, Lewis et al. (1967) reported the dominance of two polyploid races in nearly equal frequency with the narrow-leafed variety having $n = 12\pm1$ and the broad-leafed having $n = 15+3.5,-1$. Thus the diploid race $n = 7$ in Texas and the tetraploid race $n = 12$ in Missouri were typical of var. *acutiflora* whereas the tetraploid race $n = 15$ in Missouri typified the var.

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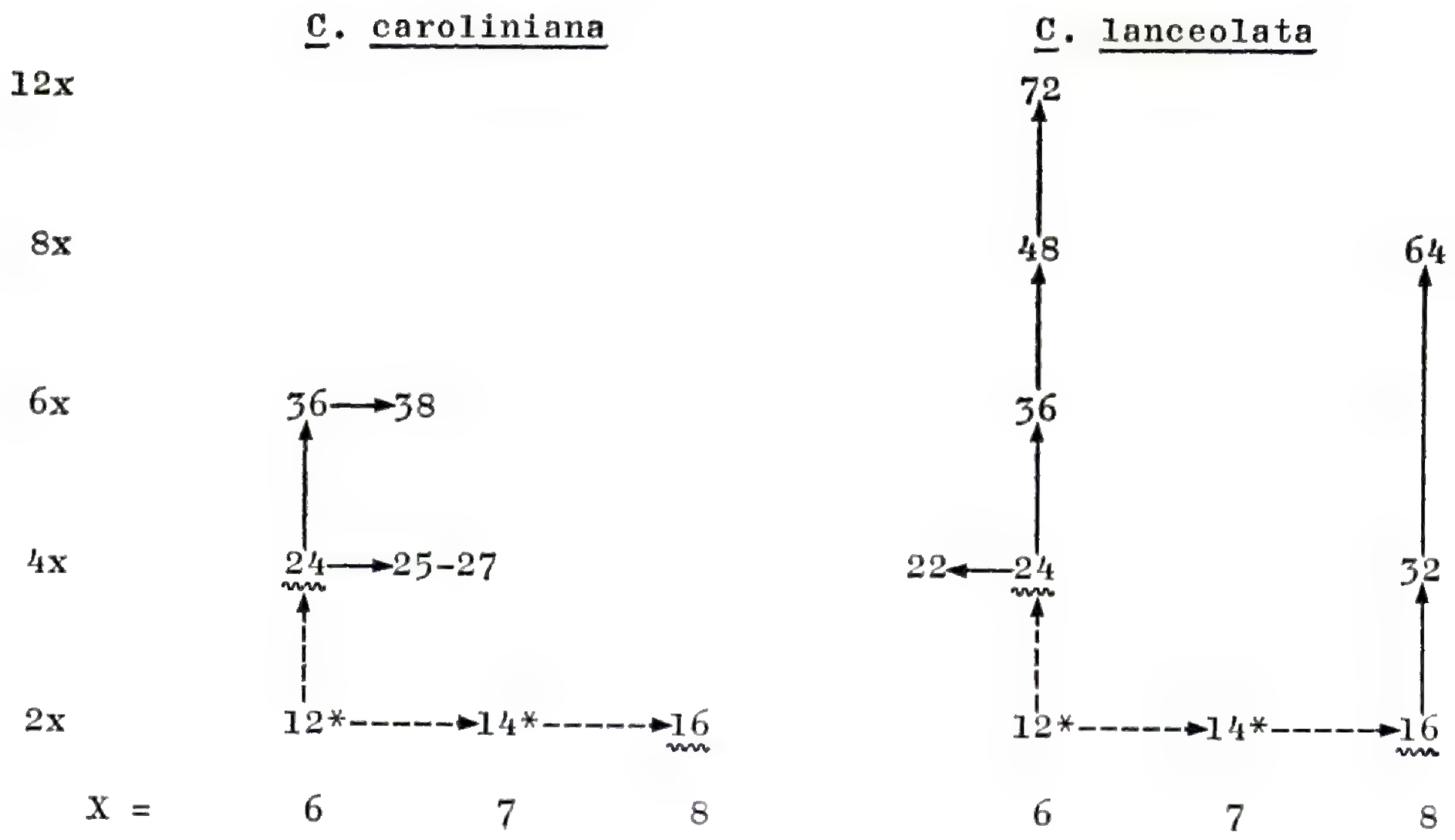
[2] Gleason & Cronquist (1963) suggested that the typical variety is probably the more southern, narrow-leafed form. Davis (1966) assumed the broad-leafed one typical, but in his revision he neither designates a lectotype nor mentions this problem.

Among three specimens mounted on one sheet collected by *Kalm s.n.* (LINN, not seen; from IDC micro-edition 285.1), the widest leaf of *C. virginica* measures 4 mm—the collection probably represents the more northern, broad-leafed variety (i.e. from Pennsylvania to the north or west, and with $n = 8$ or $16\pm$). Since Kalm returned to Sweden from eastern North America in 1751 we assume that Linnaeus saw his material before publishing the species two years later. We find no reason to ignore Kalm's collection in favor of pre-Linnaean sources, even though, for example, Linnaeus referred to the plate (*t. 102, fig.* 3) from Plukenet's Almagestum Botanicum. Plukenet clearly had the narrow-leafed *C. virginica* (width measures only 1.5 mm) and this was probably obtained from the mid or south Atlantic states (Virginia ?) with $n = 12\pm$. Thus Linnaeus included the two major elements in his *C. virginica* of which we designate *Kalm s.n.* (LINN) lectotype of the var. *virginica* with broad leaves.

For the narrow-leafed form of *C. virginica* we cannot follow Davis (1966) who named it var. *simsii* (Sweet) R. J. Davis; at least two earlier names are available at that rank. The earliest is *C. virginica* [as *virginiana*] var. *acutiflora* DC. (Prodr. **3:** 361, 1828) which includes citation of Sim's plate in Curtis's Botanical Magazine **14:** *pl. 941,* 1806 (lectotype chosen by Davis for var. *simsii*) as well as that by Plukenet. The illustration by Sim's is questionably of the narrow-leafed variety though clearly that by Plukenet is and we select his plate in the Almagestum Botanicum, *t. 102, fig.* 3, 1696, lectotype of the narrow-leafed var. *acutiflora* DC.



* unknown.

Fig. 8. Suggested evolution of the cytotypes (as $2n$) known for *Claytonia caroliniana* and *C. lanceolata*. Underscored numbers are dominant.

virginica. This suggests no correlation between leaf width and ploidy (cf. Lewis, 1967), yet a morphological-cytogeographic analysis over the range of *C. virginica* gave a different interpretation.

As summarized in Table 1 plants with $n = 6$ ($2x$) have leaf widths of $\overline{\times} = 2.0(\pm 0.1)$ mm which are similar to those with $n = 7$ ($2x$), $\overline{\times} = 2.3(\pm 0.4)$ mm. In addition plants with $n = 12 \pm 1$ ($4x$) are narrow-leafed, $\overline{\times} = 2.4$ (± 0.3) mm, as reported by Lewis et al. (1967) from the St. Louis area only. In the south, where $n = 14$ is common, $4x$ plants also have narrow leaves, $\overline{\times} = 2.3$ (± 0.9) mm. Therefore, plants having cytotypes of $n = 6$, 7, 12 ± 1, as well as 14+ in the south have very similar leaf widths from $\overline{\times} = 2.0$-2.4 mm. On the other hand significantly wider leaves are characteristic of plants with $n = 8$ ($2x$), $\overline{\times} = 5.0(\pm 0.6)$ mm, and commonly $n = 16$ ($4x$) from the north, $\overline{\times} = 5.4(\pm 0.4)$ mm, i.e. both $2x$ and $4x$ races where $x = 8$ are similar in leaf width.

Data for polyploids above the $4x$ level are scanty and the few studied form no distinct dichotomy—some with the same cytotype may have broad and narrow leaves, suggesting, as noted below, parallel evolution along narrow- and broad-leafed lines. Our sample is too small to unravel a complexity involving numerous $6x$ to $12x$ races, but consisting of only a small fraction of plants examined.

Sufficient numbers of specimens at the tetraploid level have been studied, however, to emphasize that morphology must be considered in relation to distribution and chromosome number. In the north, broad-leafed plants with $2n = 32$ are dominant in many populations; those with $2n = 30(31)$ and less commonly $2n = 28(29)$ also occur either together or at different localities, yet they

Table 1. Leaf width of plants of *Claytonia virginica* throughout its range and grouped by populational chromosome number.

Chromosome no. ($2n$)	Leaf width (mm)* $\bar{X}$	$\bar{X}s$	$\bar{X}s_{\bar{x}}$	No. of plants	No. of populations
12	2.0	0.2	0.1	14	3
12, 14	3.3	0.7	0.3	3	1
14	2.3	0.9	0.4	33	6
16	5.0	1.4	0.6	15	5
24(±2)	2.4	1.0	0.3	50	10
28-48[a]	4.2	1.9	1.1	153	30
[a]By distribution					
north (largely $2n = 32\pm2$)	5.4	1.5	0.4	57	14
central** ($2n$=28-48)	4.2	2.5	0.9	50	7
south (largely $2n = 28\pm2$)	2.3	0.9	0.3	47	9

* Calculated by populational mean of maximum leaf width per plant and reported as grand mean with standard deviation and standard error.

** ± east-west region from the southern Appalachians, central Tennessee, western Kentucky, southern Illinois, southern Missouri, to Kansas; "north" is north of this region, "south" is south of this region.

all are broad-leafed. In the south (e.g. Texas, which is the only well-sampled area) the dominant tetraploid is $2n = 28$. This race is often found near to or at the same locality with fewer plants having $2n = 29, 30, 31, 32$ etc., but in contrast to chromosomally similar plants in the north all are narrow-leafed in Texas. Using a specific example we find $2n = 30$ plants from Missouri with broad leaves, but plants with the same chromosome number from Texas have narrow leaves. Apparently their evolutionary pathways were quite distinct: the first as secondary tetraploids from the broad-leafed $x = 8$ line common in the Midwest (perhaps $n = 8+8-1$), the second also as secondary tetraploids but from the narrow-leafed $x = 7$ line dominant in Texas (perhaps $n = 7+7+1$). Both gave rise to plants having $2n = 30$, but one subrace arose via a broad-leafed northern $x = 8$ complex and the other in a parallel way from the narrow-leafed southern $x = 7$ complex.

In summary *C. virginica* has evolved from an ancestral narrow-leafed race having $n = 6$ from which the widespread $n = 12\pm$ and southern $n = 7$ races arose. From the latter was derived a $n = 14$ race also common in the south. These races and at least some of their higher polyploid derivates make up the narrow-leafed var. *acutiflora*. From continuing autoaneuploidy at the diploid level evolved the $n = 8$ race where, we believe, particular chromosomal redundancies with cer-

tain genetic combinations or duplications lead to the expression of broad leaves. Such plants became widespread in the north as did the morphologically similar $n = 16\pm$ race. These races and their derivatives, largely aneutetraploids, represent the more recently evolved broad-leafed var. *virginica*.

We agree with Davis (1966) that no other gross morphological feature correlates with leaf width. We found no obvious trend in petal and sepal size or shape, corm size, and size or number of floral stems per plant. For one "micromorphological" character, size of seed, a certain tendency was noted although this observation is based on limited material. Seeds from plants with $n = 6$ and 7 measure about 1.5 mm in diameter while those from $n = 8$ plants and the primary tetraploids are slightly larger, 1.7-2.0 mm. This size tendency parallels somewhat that of leaf width, but the maximum diameter is such that it precludes great usefulness apart from the fact that many of our vouchers and herbarium material generally lack seeds.

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CHROMOSOME NUMBERS IN COMPOSITAE. XI. PERUVIAN SPECIES[1]

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ABSTRACT

Chromosome counts are reported for 60 collections of Peruvian *Compositae* representing 59 species in 31 genera. Most of these are first reports for a taxon concerned, including the genera *Ascidiogyne* ($n = 10$), *Diplostephium* ($n = 9$), *Oriotrophium* ($n = 9$), *Achyrocline* ($n =$ ca 14), *Gynoxys* ($n = 40$), *Loricaria* ($n =$ ca 14), *Monopholis* (n = ca 30) and *Pappobolus* ($n = 17$). Supernumerary or "B" chromosomes have been found in *Baccharis and Monopholis,* and an unusual aneuploid series has been detected in *Liabum* ($x = 9$, 12, 14, and ca 18).

Chromosome counts for 60 collections of Peruvian *Compositae* are presented in Table 1. Bud material was collected in the field by Dr. John Wurdack and airmailed to the senior author in Austin, Texas, where the counts were made by the usual squash techniques (Turner & Johnston, 1959). Since most of these collections were from remote areas, it was often several weeks before the fixed material could be mailed. These delays and the high temperatures to which the meiotic material was exposed probably account for the numerous approximate counts reported in this paper. (Label-data on the voucher specimens—deposited TEX, US—give approximate counts, plus or minus 1 or 2 chromosomes; in Table 1 we have listed all such counts as approximations only.) Identifications were made by J. Cuatrecasas except for those of *Bidens* and *Coreopsis* (by the late E. E. Sherff), *Hypochaeris* (by A. L. Cabrera) and *Liabum rugosum* (by R. Ferreyra); chromosome counts were made by Powell and Turner, either singly or in combination.

RESULTS AND DISCUSSION

VERNONIEAE—*Vernonia baccharoides* ($n =$ ca 17) and *V. pacchensis* ($n =$ ca 8): Hunter (1964) reported several species of the sect. *Lepidoploa* of *Vernonia* with chromosome numbers of $n = 17$. Jones & Duncan (1966), however, reported chromosome numbers of $n = 18$ for numerous species, including at least three of the taxa investigated by Hunter. Unfortunately the meiotic figures from which our counts were made were not sufficiently clear to allow unequivocal counts, although the approximate counts are believed to be accurate within one chromosome pair.

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Table 1. *Compositae* of Peru (Departmento Amazonas) examined for chromosome number.

Species	Locality and Voucher	*n* Number[a]	
TRIBE VERNONIEAE			
Vernonia baccharoides H.B.K.	Prov Bagua, *Wurdack 1812*	17	
Vernonia pacchensis var. *tambillensis* Hieron.	Prov Chachapoyas, *Wurdack 715*	ca 8	
TRIBE EUPATORIEAE			
Ageratum latifolium Cav.	Prov Chachapoyas, *Wurdack 443*	20	
Ascidiogyne wurdackii Cuatr.	Prov Chachapoyas, *Wurdack 1716*	10	
Ascidiogyne wurdackii Cuatr.	Prov Chachapoyas, *Wurdack 1246*	ca 10	
Mikania speciosa DC.	Prov Chachapoyas, *Wurdack 770*	ca 16	
Mikania violaefolia Cuatr.	Prov Chachapoyas, *Wurdack 1257*	ca 18	
Eupatorium pseudarboreum Hieron.	Prov Chachapoyas, *Wurdack 468*	10	
Eupatorium ivaefolium var. *hirsutum* Hass.	Prov Chachapoyas, *Wurdack* 647	50	I
Eupatorium macrophyllum L.	Prov Bagua, *Wurdack 1815*	10	
Eupatorium ventillanum Cuatr.	Prov Chachapoyas, *Wurdack 1476*	ca 17	
Eupatorium weberbaueri Hieron.	Prov Bongará, *Wurdack 988*	10	
Stevia andina Rob.	Prov Chachapoyas, *Wurdack 417*	ca 22	
Stevia rhombifolia H.B.K. var *stephanocoma* Sch. Bip.	Prov Chachapoyas, *Wurdack 445*	ca 46	I
TRIBE ASTEREAE			
Baccharis chachapoyasensis Cuatr.	Prov Chachapoyas, *Wurdack* 597	ca 9	
Baccharis chilco H.B.K.	Prov Chachapoyas, *Wurdack 496*	9	
Baccharis decussata (Klatt) Hieron.	Prov Bongará, *Wurdack 836*	9[b]	(Fig. 1)
Baccharis genistelloides (Lam.) Pers.	Prov Chachapoyas, *Wurdack 498*	9	
Baccharis grandicapitulata Hieron.	Prov Chachapoyas, *Wurdack 664*	9	
Baccharis latifolia (R. & P.) Pers.	Prov Chachapoyas, *Wurdack 455*	ca 18	
Baccharis oblongifolia (R. & P.) Pers.	Prov Chachapoyas, *Wurdack 1645*	9	
Baccharis phylicoides H.B.K.	Prov Chachapoyas *Wurdack 548*	ca 9	
Baccharis spathulata Klatt	Prov Chachapoyas, *Wurdack 1377*	9	
Baccharis tricuneata fma. *callaensis* Cuatr.	Prov Chachapoyas, *Wurdack 1706*	10	?
Diplostephium konotrichum Cuat.	Prov Chachapoyas, *Wurdack 1634*	9	
Diplostephium wurdackii Cuatr.	Prov Chachapoyas, *Wurdack 1672*	9	(Fig. 2)
Erigeron lanceolatus Wedd. var. *subacaule* Wedd.	Prov Chachapoyas, *Wurdack 792*	27	
Oritrophium aciculifolium Cuatr.	Prov Chachapoyas, *Wurdack 1275*	9	(Fig. 3)
TRIBE INULEAE			
Achyrocline alata (H.B.K.) DC.	Prov Chachapoyas, *Wurdack 726*	ca 14	
Gnaphalium spicatum Lam.	Prov Chachapoyas, *Wurdack 1699*	14	
Loricaria thuyoides (Lam.) Sch. Bip. var. *thuyoides*	Prov Chachapoyas, *Wurdack 1188*	ca 14	
TRIBE HELIANTHEAE			
Bidens pilosa var. *calcicola* (Greenm.) Sherff	Prov Chachapoyas, *Wurdack 444*	ca 24	
Bidens laevis (L.) B.S.P.	Prov Bongará, *Wurdack 892*	12	
Bidens triplinervia var. *mollis* (P. & E.) Sherff	Prov Chachapoyas, *Wurdack 488*	12	
Calea jelskii Hieron.	Prov Chachapoyas, *Wurdack 712*	19	(Fig. 4)
Coreopsis microlepis Blake & Sherff	Prov Chachapoyas, *Wurdack 472*	13	
Franseria artemisioides Wedd.	Prov Chachapoyas, *Wurdack 442*	ca 18	
Jaegeria hirta (Lag.) Less.	Prov Chachapoyas, *Wurdack 435*	ca 18	
Monopholis jelskii (Hieron.) Blake	Prov Chachapoyas, *Wurdack 452*	ca 30[b]	(Fig. 5)
Pappobolus woodsonianus Cuatr.	Prov Chachapoyas, *Wurdack 584*	17	
Siegesbeckia mandonii Sch. Bip.	Prov Bongará, *Wurdack 1009*	ca 30	
Spilanthes americana (Mutis) Hieron.	Prov Chachapoyas, *Wurdack 416*	ca 26	
Viguiera brittonii Hochreut.	Prov Chachapoyas, *Wurdack 414*	ca 34	
Wedelia helianthoides H.B.K.	Prov Chachapoyas, *Wurdack 448*	ca 20	
TRIBE SENECIONEAE			
Gynoxys parvifolia Cuatr.	Prov Chachapoyas, *Wurdack 1702*	ca 40	
Gynoxys tomentosissima Cuatr.	Prov Chachapoyas, *Wurdack 1254*	40[b]	
Liabum bullatum (Gray) Hieron.	Prov Chachapoyas *Wurdack 1240*	9	

Table 1. (*Cont.*)

Species	Locality and Voucher	*n* Number[a]	
Liabum hieracioides (H.B.K.) Less.	Prov Chachapoyas, *Wurdack 793*	12	(Fig. 6)
Liabum rugosum Ferreyra	Prov Chachapoyas, *Wurdack 469*	ca 18	
Schistocarpha oppositifolia (Ktze.) Rydb.	Prov Bagua, *Wurdack 1814*	ca 8	
Schistocarpha sinforosii Cuatr. fma.	Prov Chachapoyas, *Wurdack 796*	8	
Senecio coymolachensis Cabrera	Prov Chachapoyas, *Wurdack 1559*	20	
Senecio jalcanus Cuatr.	Prov Chachapoyas, *Wurdack 1375*	50	
Senecio loeseneri Hieron.	Prov Chachapoyas, *Wurdack 802*	20	
Senecio pleniauritus Cuatr.	Prov Chachapoyas, *Wurdack 1669*	ca 40	
Senecio verticillatus Klatt var. *trichophorus* Greenm.	Prov Chachapoyas, *Wurdack 799*	ca 45	
Senecio wurdackii Cuatr.	Prov Chachapoyas, *Wurdack 1599*	ca 40	
Werneria stuebelii Hieron.	Prov Chachapoyas, *Wurdack 1551*	50	(Fig. 7)
TRIBE MUTISIEAE			
Mutisia wurdackii Cabrera	Prov Bongará, *Wurdack 840*	ca 23	
TRIBE CICHORIEAE			
Hypochaeris sessilifolia H.B.K. vel sp. nov. *affinis*	Prov Chachapoyas, *Wurdack 437*	6	

[a] Unless indicated to the contrary the numbers listed refer to chromosome *pairs;* univalents are indicated by the Roman numeral I.

[b] Indicates that "B" chromosomes and/or fragments were observed.

EUPATORIEAE—*Ascidiogyne* ($n = 10$), is a recently described genus belonging to the subtribe *Piquerinae* (Cuatrecasas, 1965). *Piqueria* itself is at least tribasic, possessing species with haploid numbers of 10, 11 and 12 (Cave 1956-64). The only other genus of *Piquerinae* for which counts are available is *Adenostemma* with $x = 5$ (Turner & Irwin, 1960). The tribe *Eupatorieae* contains approximately 40 genera; counts are available for only 10, establishing *n* numbers of 4, 5, 9, 10, 11, 12, 15, 17, 18, 19. The most frequently encountered base number is $x = 10$ (6 genera), this being found in all three subtribes of the *Eupatorieae.*

Chromosome counts for the genera *Ageratum* ($x = 10$), *Eupatorium* ($x = 10, 17$), and *Stevia* ($x = 11, 17$) are consistent with base numbers already established for these genera (Cave, 1956-64). The approximate count for *Stevia rhombifolia* var. *stephanocoma* ($n = 46$ univalents) is interesting in that Powell & Turner (1963) report a number of $n = 34$ univalents for collections of this species from Mexico. Univalents in meiotic material are also found in species possessing base numbers of $x = 11$ (Turner & Flyr, 1966); thus it is difficult to evaluate the approximate count of 46 univalents listed for the South American collections of *S. rhombifolia,* although $n = 51$ univalents would appear to be the most logical interpretation as to its correct number, if the relationship of the varietal taxon is correct.

ASTEREAE—*Baccharis* ($x = 9$) is a large shrubby genus with several hundred species. Including the 10 species listed in Table 1, chromosome counts are now available for about 30 species. All counts have been diploid ($n = 9$) with the exception of *B. latifolia* ($n =$ ca 18, Table 1). *Baccharis tricuneata* is listed here

as having a questionable count of $n = 10$; while the meiotic plate seemed unequivocal it is possible that a supernumerary or "B" chromosome was mistaken as a bivalent. Such chromosomes are found in *Baccharis*, for *B. decussata* possesses 9 large, dark-staining bivalents and 4 smaller, heterochromatic "B" chromosomes (Fig. 1).

Chromosome counts for *Diplostephium* ($n = 9$) and *Oritrophium* ($n = 9$) are first reports. The latter is often included in *Erigeron* as a section but chromosomally (by its very large bivalents) and morphologically it seems sufficiently distinct to warrant generic rank.

INULEAE—*Achyrocline* ($n =$ ca 14), *Gnaphalium* ($n = 14$) and *Loricaria* ($n =$ ca 14) belong to the subtribe *Filagininae*, the genera of which are mostly $x = 7$. While the latter number is relatively common in this tribe, recent sampling from Australia, where the *Inuleae* are perhaps best developed, has revealed a considerable range of base numbers, from $x = 3$ to $x = 14$ (Turner, unpublished).

HELIANTHEAE—Chromosome counts for species of *Bidens* ($n = 12$, ca 24), *Calea* ($n = 19$), *Coreopsis* ($n =$ ca 30), *Franseria* ($n =$ ca 18), *Jaegeria* ($n =$ ca 18), *Siegesbeckia* ($n =$ ca 30), *Spilanthes* ($n =$ ca 26), *Viguiera* ($n =$ ca 34) and *Wedelia* ($n =$ ca 20) are consistent with the base numbers reported for these genera by earlier workers. It should be noted that the base number for *Spilanthes*, as established by Turner et al. (cf. Cave, 1956-64), appears to be $x = 13$. However, Cave (1964) lists a count for *Spilanthes acumella* as $n = 7$, although Mehra et al. (1965) report the species to have $n = 12$. The photograph of meiotic material which accompanied the latter report is not particularly convincing since at least some of the chromosomes which they picture seem to be clumped; consequently we prefer to accept the monobasic number $x = 13$ until more convincing documentation is forthcoming.

Pappobolus woodsonianus ($n = 17$) is a recently described species (Cuatrecasas, 1965) belonging to the subtribe *Verbesininae*. It has been compared to species belonging to *Helianthus*, a genus which also possesses species with a base of $x = 17$.

Monopholis ($n =$ ca 30), according to Blake (1922), is related to both *Verbesina* and *Monactis*, but perhaps closer to the latter. Chromosomally, *Monopholis jelskii* is distinguished by its relatively large bivalents and "B" chromosomes (Fig. 5). *Monactis* has not been examined but *Verbesina* (15 or more species investigated) is at least tribasic with $x = 16$, 17 and 18 while "B" chromosomes are unreported (Turner, Beaman & Rock, 1961; Turner & Flyr, 1966).

SENECIONEAE—*Gynoxys* with diploid chromosome numbers of 80 or near 80 appears to have a base of $x = 10$, although seemingly unequivocal counts were obtained from only one of the three species examined (Table 1).

Liabum (sensu lato) is a heterogenous group, the included species showing markedly different involucral types (uni- to multiseriate) and habits (small herbs to shrubs). Chromosomally the genus is also heterogeneous, for we have obtained

Fig. 1-7. Camera lucida drawings of meiotic chromosomes × 2700. Fig. 1. *Baccharis decussata* ($n = 9$), note the 4 supernumerary chromosomes (stippled). Fig. 2. *Diplostephium wurdackii* ($n = 9$). Fig. 3. *Oritrophium aciculifolium* ($n = 9$). Fig. 4. *Calea jelskii* ($n = 19$). Fig. 5. *Monopholis jelskii* ($n =$ ca 30), note the 8 or 9 supernumerary chromosomes (stippled). Fig. 6. *Liabum hieracioides* ($n = 12$), note the unusually large bivalent. Fig. 7. *Werneria stuebellii* ($n = 50$).

counts of $n = 9$, 12 and ca 18 for the three species listed in Table 1. The only previous count has been that of Diers (1961) who reported $2n = 28$ for *Liabum ovatum*. The chromosomes of *L. hieracioides* ($n = 12$) were especially interesting in that one very large bivalent, 3 to 5 times larger than the others, was seen consistently at metaphase I of meiosis (Fig. 6). The chromosomal data, scant as these are, would appear to justify the treatment of at least some of Bentham's sections (1873) as genera, for the several taxa we have examined belong to different subgeneric groupings.

Werneria stuebelii ($n = 50$) is the second report of an established count for this genus; Beaman & Turner (1962) having reported a count of $n = 50$ for *W. nubigena*. The only other counts have been those of Diers (1961) who reported a range of approximate counts for *Werneria* spp. ($n =$ ca 21, 50, 52, 53, 54, 75, 77, 103, 106) and that of Heiser (1963) who reported a count of $n =$ ca 48 for *W. nubigena*. Apparently the genus has a base number of $x = 25$ from an ancestral base of $x = 5$ (Turner & Lewis, 1965).

Chromosome numbers for *Schistocarpa* ($n = 8$) and *Senecio* ($n = 20$, ca 45, 50) are consistent with the base numbers established for these genera by several workers (Cave, 1964; Turner & Lewis, 1965; Ornduff et al., 1967).

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CHROMOSOME NUMBERS OF PHANEROGAMS. 2.

Chromosome numbers of phanerogams are reported below together with the voucher data and the herbaria where collections are deposited. Unless indicated the chromosomal records are based on the study of one plant. Haploid counts are from pollen mother cells and diploid counts are from root tips unless otherwise indicated. An asterisk indicates that one or more permanent slides are available at the Missouri Botanical Garden Herbarium.

The authors responsible for chromosome counts are listed alphabetically. Citation should have the form of: Doe, J, 1967. *In* Chromosome numbers of phanerogams. 2. Ann. Missouri Bot. Gard. **54:** pp.

BY THOMAS S. ELIAS

LEGUMINOSAE

Canavalia oxyphylla Standley & Williams: **2n = 22.** British Honduras: Stann Creek, S of Lynam Agricultural College, along stream, *Dwyer et al. 551* (MO, SIU).

Cracca greenmanii Millsp.: **2n = 16.** British Honduras: Cayo, SW of Cayo at summit of Mayan Ruins, *Dwyer et al. 257* (MO, SIU).

Crotalaria retusa L.: **2n = 16.** British Honduras: Belize, edge of road nr St. John's College, *Dwyer et al. 12* (MO, SIU).

BY WALTER H. LEWIS, YUTAKA SUDA, AND ROYCE L. OLIVER[1]

COMMELINACEAE

Aneilema cf. *beniniense* (P. Beauv.) Kunth: **2n = 52***. Seeds from Antwerp Bot Gard [originally tropical Africa], cultivated Missouri Bot Gard (66-7-2), voucher *Lewis* 6835 (MO).

Aneilema geniculatum (Jacq.) Woodson: **n = 16, 2n = 32***. Panama: Canal Zone, ca 19 mi from Colón, *Burch et al. 1048* (GH, K, MO, UC, US).

Aneilema ovato-oblongum P. Beauv.: **n = 13***, **2n = 26***. Panama: Bocas del Toro Prov, Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2027* (MO). This species is newly recorded for Panama and Central America.

Aneilema papuanum Warb.: **2n = 32***. Seeds from Antwerp Bot Gard [originally Papua], cultivated Missouri Bot Gard (65-25-1), voucher *Lewis* 6836 (MO).

Callisia repens L.: **2n = 14***. Panama: Chiriquí Prov, Boquete vic to 3 mi N, *Lewis et al. 403* (F, GH, K, MO, NY, US). This species is newly reported for Panama.

Campelia zanonia (L.) H.B.K.: **2n = 16***—Fig. 1. Panama: Bocas del Toro Prov, 10-15 mi S from mouth of Changuinola River, *Lewis et al.* 883 (MO);

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[1] Collecting of seeds and living plants was aided by grants from the National Science Foundation (GB-5674) and the Air Force Office of Scientific Research (F44620-67-C-0055).

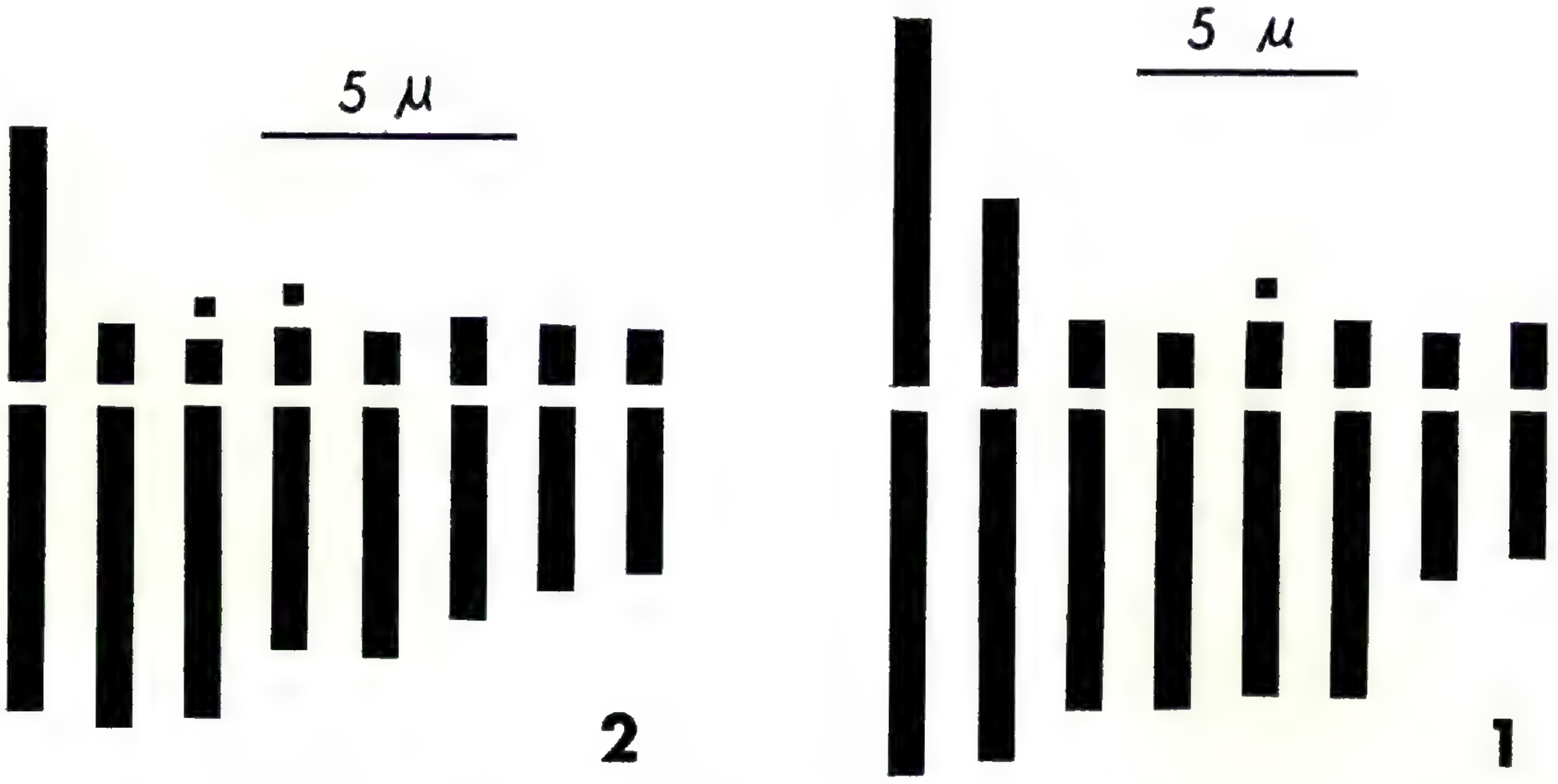

Fig. 1-2. Idiograms of *Campelia* and *Tripogandra* drawn from photographs originally at 4,500× (root tips pretreated with 0.1% colchicine for 1½ hr). Fig. 1. *C. zanonia* (*Lewis et al.* 833), $2n = 16$. Fig. 2. *T. pflanzii* (*Lewis* 6841), $2n = 16$.

Chiriqui Prov, Boquete vic to 3 mi N, *Lewis et al. 414* (GH, MO, US). Following pretreatment the chromosomes range from 4.8-16.5μ in length (Fig. 1) with the longest pair median, one submedian pair and six smaller subterminal pairs including a pair with satellites. This karyotype differs from that described by Darlington (Jour. Genet. **35:** 259-280, 1938) who found two large median pairs of chromosomes. This suggested to him a tetraploid condition and a basic number of 4 for *C. zanonia*, judgements which become questionable with our finding of only one median pair of chromosomes.

Cochliostemma jacobianum Koch & Linden: **2n = 38***. Cultivated Missouri Bot Gard (60-125-1) [originally Ecuador?], voucher *Lewis* 6837 (MO).

Commelina diffusa Burm. f.: **2n = 30***. Panama: Chiriquí Prov, Boquete vic to 3 mi N, *Lewis et al. 403* (F, GH, K, MO, NY, US); Venezuela: Miranda St, first creek S of Cúa, *Robertson & Austin 146* (MO).

Commelina sikkimensis C. B. Cl.: **2n = 90***. Seeds from Copenhagen Bot Gard [originally Sikkim], cultivated Missouri Bot Gard (65-58-1), voucher *Lewis* 6838 (MO).

Commelina virginica L.: **2n = 60***. Peru: Loreto Dept, Iquitos, bank overlooking Amazon River, *Robertson & Austin 61* (MO); Venezuela: Miranda St, rd from Chirimena to Chuspa, *Robertson & Austin 220* (MO), ca 25 km S of Caracas, *Robertson & Austin 127* (MO).

Siderasis fuscata (Lodd.) H. E. Moore: **n = 19***, **2n = 38***. Cultivated Missouri Bot Gard (65-106-8) [originally Brazil], voucher *Lewis* 6839 (MO).

Tradescantia blossfeldiana Mildbr.: **n = ca 36, 2n = 72***. Cultivated Missouri Bot Gard [originally Argentina?], voucher *Lewis* 6840 (MO).

Tradescantia commelinoides Roem. & Schult.: **2n = 38***. Panama: Chiriquí Prov, Boquete vic to 3 mi N, *Lewis et al. 405* (GH, K, MO, UC, US).

Tripogandra cumanensis (Kunth) Woodson: **2n = 39***. Panama: San Blas Prov, mainland opposite Ailigandi, *Lewis et al. 202* (GH, MO, UC, US).

Tripogandra elongata (G. F. W. Meyer) Woodson: **n = 24***, **2n = 48***. Panama: Chiriquí Prov, Boquete vic to 3 mi N, *Lewis et al. 404* (F, GH, K, MO, NY, UC, US); Coclé Prov, hills NE of El Valle, *Lewis et al. 1789* (MO); Panama Prov, 2-3 mi S of Goofy Lake on rd to Cerro Jefe, *Lewis et al. 243* (GH, K, MO, UC, US).

Tripogandra pflanzii (Brüchn.) Rohw.: **n = 8***, **2n = 16***—Fig. 2. Seeds from Marburg Bot Gard [originally Bolivia], cultivated Missouri Bot Gard (66-24-3), voucher *Lewis 6841* (MO). Following pretreatment the chromosomes range from 4.3-10.7μ in length with one long median pair and seven much shorter subterminal pairs, two pairs of which have satellites.

Tripogandra warscewicziana (Kunth & Bouché) Woodson: **n = 8.** Cultivated Missouri Bot Gard, count made by Dr. Edgar Anderson, 4 Apr 1942, voucher MO 1063396.

CONVOLVULACEAE

Ipomoea alba L.: **2n = 30**. Peru: Loreto Dept, 5 km N of Iquitos, *Robertson & Austin 48* (MO).

Ipomoea nil (L. emend. Curtis) Roth: **2n = 30***. Seeds from G. W. Park Seed Co, Greenwood, South Carolina, received as *I. volubilis gigantea,* progeny *Lewis 6482* (MO, SMU), received as *I.* 'fancy fringed,' progeny *Lewis 6484* (MO, SMU).

Ipomoea stolonifera (Cry.) Gmel.: **2n = 30**. British Honduras: Toledo Distr, Punta Gorda, *Dwyer et al. 605* (MO).

Ipomoea sp.: **2n = 30**. Peru: Loreto Dept, Yanayacu, across Amazon River E of Iquitos, *Robertson & Austin 95* (MO).

Ipomoea sp.: **2n = 30**. Venezuela: Miranda St, rd to Santa Teresa, ca 5 km from Autopista, *Robertson & Austin 195* (MO).

Iseia luxurians (Moric.) O'Donell: **2n = 60**. Panama: Herrera Prov, rd from Chitré to Divisa, *Burch et al. 1360* (MO).

Merremia aegyptia (L.) Urban: **2n = 28.** Panama: Herrera Prov, rd from La Avena to outskirts of Pese, *Burch et al. 1292* (MO).

Merremia umbellata (L.) Hall. f.: **2n = 28***. British Honduras: Toledo Distr, Punta Gorda, *Dwyer et al. 636* (MO); Venezuela: Miranda St, ca 2 km S of Charallave, *Robertson & Austin 144* (MO).

PORTULACACEAE

Claytonia spathulata Dougl. ex Hook.: **n = 8**. California: Santa Clara Co, San Antonio Valley Rd, *Lewis 6644* (MO). This species is reported by Nilsson (Bot. Not. **119:** 464-468, 1966) from British Columbia with $2n = 48$; the closely allied if not conspecific *C. gypsophiloides* Fisch. & Mey. is, however, also known with $2n = 16$ (Nilsson, loc. cit.).

Montia chamissoi (Ledeb. ex Spreng.) Robins & Fern.: **n = 11**. Idaho: Custer Co, 10.5 mi NNW of Mt Borah by Hwy 93A (in "Miniature Grand Canyon"),

Lewis 6769 (GH, LE, MO, UC). From field notes: "medium to small sized bivalents similar in size to those of *M. parvifolia*."

Montia parvifolia (Mocino ex DC.) Greene: **n = 11**. Montana: Missoula Co, 9.4 mi N of Missoula (from Blackfoot River) along Rattlesnake Creek, *Lewis 6764* (MO), 2 plants.

ROSACEAE

Rosa moschata var. *abyssinica* (Lindl.) Rehder: **2n = 14***. Plant from U. S. National Arboretum (26783) [originally Ethiopia], cultivated Missouri Bot Gard, voucher *Lewis 6842* (MO).

RUBIACEAE

Borreria verticellata (L.) G. F. W. Meyer: **2n = 28***. Venezuela: Guárico St, ca 8 km SE of Llanos Biol Sta, *Robertson & Austin 164* (MO).

Hedyotis diffusa Willd.: **2n = 32***. Taiwan: Taipei Co, Suh Ting, *Huang 4013*, seeds from Dr. T. C. Huang, progeny *Lewis 6790* (MO); Taipei, *Huang 3941*, seeds from Dr. T. C. Huang, progeny *Lewis 6788* (MO).

Hedyotis nantoensis Hayata: **2n = 32**. Taiwan: Nantou Co, Sun Moon Lake, *Huang 4016*, seeds from Dr. T. C. Huang, progeny *Lewis 6792* (MO). Doubtfully distinct from *H. diffusa*.

Neanotis hirsuta var. *glabricalycina* (Honda) W. H. Lewis: **2n = 36***. Taiwan: Taipei Co, Suh Ting, *Huang 4012*, seeds from Dr. T. C. Tuang, progeny *Lewis 6791* (MO).

BY JOAN W. NOWICKE

NYCTAGINACEAE

Bougainvillea spectabilis Willd.: **2n = 34**. Missouri: St. Louis, cultivated Missouri Bot Gard, *Nowicke 80* (MO).

PHYTOLACCACEAE

Rivina humilis L.: **2n = 108**. Missouri: St. Louis, cultivated Missouri Bot Gard, *Nowicke 77* (MO).

NOTES

A NEW SPECIES OF EUPHORBIA FROM PANAMA

Recent collections from the edge of a cloud forest at about 5500 ft on Cerro Horqueta included one unfamiliar *Euphorbia*. It has a superficial resemblance to species of Boissier's sect. *Dichilium* or sect. *Alectoroctonum*, but is easily distinguished from these by the non-articulate stems and by the smooth seed coat. This smooth seed coat, in fact, makes it difficult to assign it to any of the existing subdivisions of the genus, and suggestions as to its relationship must await further studies in this disparate group.

Euphorbia **dwyeri** Burch, sp. nov.—Fig. 1.

Herba caulibus ascendentibus teretibus ad 1.5 m longis sparse ramosis. *Folia* petiolata, inferiora alterna, superiora opposita (supra verticillum trifoliatum); stipulae obsoletae; lamina ovato-lanceolata, glabra. *Cyathium* infundibuliforme vel campanuliforme; glandulae 4, appendicibus glandulas aequantibus, supra pilis rigidis patentibus. *Capsula* late ovoidea, glabra; semina ecarunculata, ovoidea, laevia.

Herb, sparingly branched from a somewhat thickened rootstock, stems terete, sprawling, to 1.5 m long, green, glabrous, not articulated. *Leaves* alternate through much of stem, opposite above a 3-leaved whorl; stipules obsolete; petiole slender 2.5-6 cm long; blade ovate-lanceolate, 3.5-6 × 2-3.5 cm, thin, base cuneate to rounded, sometimes obscurely peltate, margin entire, apex obtuse to rounded or emarginate and mucronulate, green (drying darker above than below), glabrous except for scattered short hairs in the under surface. *Cyathia* terminal in groups of 2-5 (rarely more) on short dichotomizing branches (formed mostly above but occasionally below whorl of 3 leaves), funnelform-campanulate, 2 mm long, 2 mm in diam; peduncle to 4 mm long; bracts slightly exceeding glands, glabrous without except for short hairs near apex, densely pubescent within; glands 4, dark, broadly elliptic, appendages as broad as glands, margin obscurely crenulate, short pubescent below and glabrate, stiffly pubescent above near gland simulating a ciliate edge to gland or rarely glabrous. *Staminate flowers* 5-12, naked, glabrous. *Pistillate flower* naked, glabrous, ovary obovoid, styles 3, joined for lower 1/3, bifid for ca 1/4 length. *Capsule* broadly ovoid, 4 mm long, 4 mm in diam, glabrous; seed ecarunculate, ovoid, 3 mm long, smooth.

Panama. chiriquí: NW of Boquete, Cerro Horqueta, alt 5000-5800 ft, trail to lower edge of cloud forest, 13 Dec 1966, *Dwyer, Elias, Escobar & Oliver 434* (holotype MO; isotypes GH, K, US).

—*Derek Burch, Missouri Botanical Garden, St. Louis.*

Ann. Missouri Bot. Gard. **54**(2): 182-200, 1967.

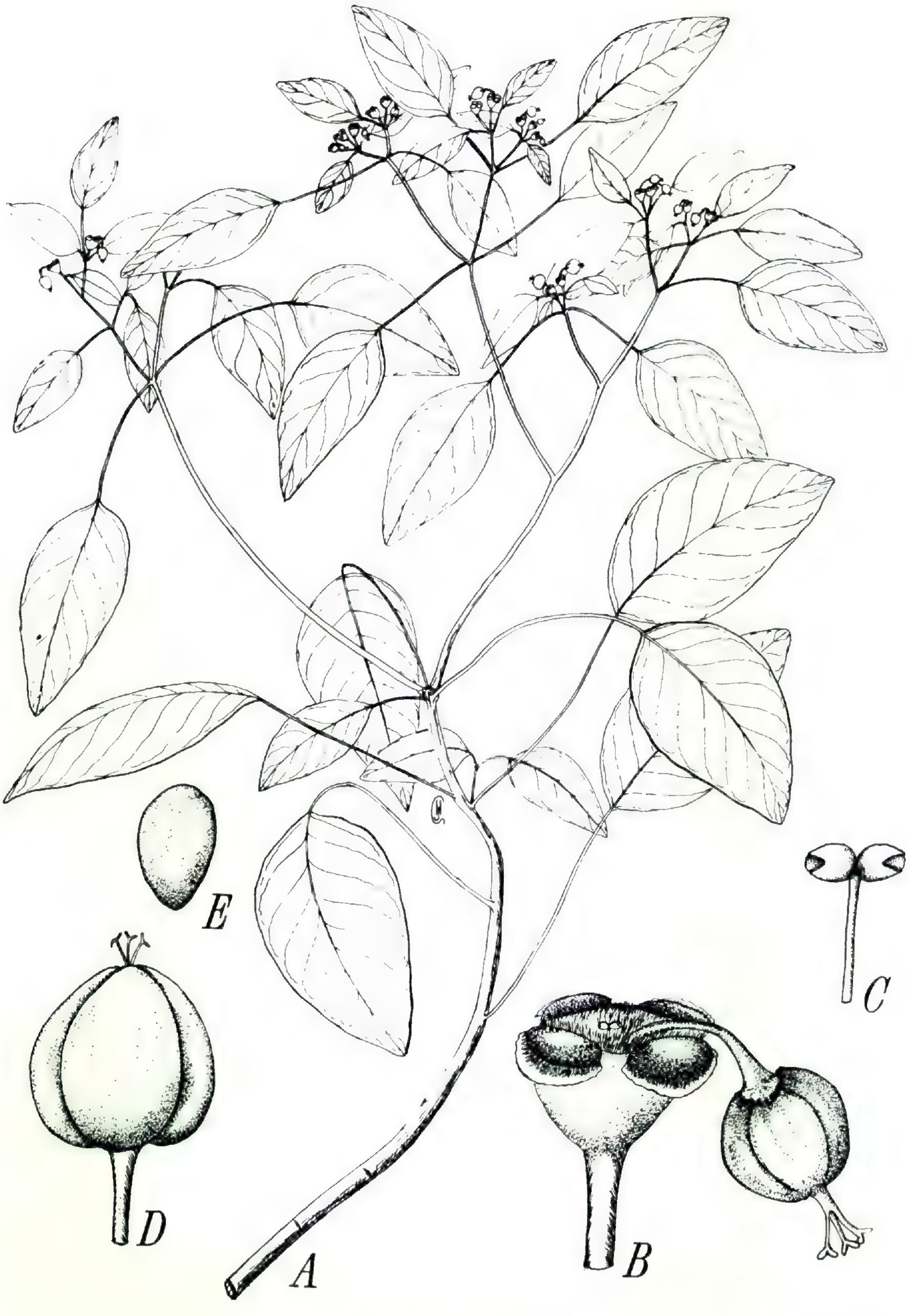

Fig. 1. *Euphorbia dwyeri* Burch: A, habit (ca ×1); B, cyathium (ca ×16); C. stamen (ca ×40); D, capsule (ca ×10); E, seed (ca ×10). After *Dwyer et al.* 434.

CORRECTION: CHAMAESYCE OPHTHALMICA (PERS.) BURCH

I am indebted to Dr. C. D. Adams of the Department of Botany, University of the West Indies, Jamaica, for pointing out my carelessness when making the transfer of Persoon's *Euphorbia ophthalmica* to the genus *Chamaesyce* (Ann. Missouri Bot. Gard. **53:** 98, 1966). My spelling "opthalmica" was incorrect and the combination should read *Chamaesyce ophthalmica* (Pers.) Burch.—*Derek Burch, Missouri Botanical Garden, St. Louis.*

ILEX VALERII VAR. RAMONENSIS (STANDLEY) EDWIN, STAT. NOV. (AQUIFOLIACEAE)

Ilex valerii Standley var. **ramonensis** (Standley) Edwin, stat. nov., based on *I. ramonensis* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 630, 1937.—*Gabriel Edwin, Field Museum of Natural History, Chicago, Illinois.*

BOMBACACEAE NEOTROPICAE NOVAE I. NEW SPECIES OF CHORISIA AND QUARARIBEA.

Chorisia **incana** A. Robyns, sp. nov.; *C. integrifoliae* Ulbr. proxima, a qua tubi staminei parte incrassata inferiore ut verticillo loborum anatherorum dense stellato-incana sat differt.—Fig. 1.

Arbor usque ad 10 m alta; truncus 60 cm diam attingens; rami ramulique glabri et inermes. *Folia* alterna, ramulorum apicem versus glomerata, digitata, 5-foliolata, glabra; petiolus teres, longitudinaliter sulcatus, basi apiceque vix dilatatus, usque ad 10 cm longus; foliola breviter petiolulata petioluloque usque ad 3-5 mm longo supra canaliculato ad petiolum articulato; lamina elliptica, basi attenuata et in petiolulum decurrens, apice caudato-acuminata acumineque plus minusve obtuso et mucronulato, usque ad 11 cm (vel ultra?) longa et 5.5 cm lata, chartacea, marginibus integris, supra nitida, subtus opaqua, nervo mediano supra carinato-prominulo infraque prominenti, nervis secundariis utrinque subprominulis. *Flores* ad ramulorum apicem aggregati, axillares, solitarii (?) vel 2-3-fasciculati; albastra oblonga, apice rotundata; pedicellus rectus, plus minusve angulatus, usque ad 3.5 cm longus, in sicco nigrescens, glaber, in parte superiore 3 bracteolis alternatis cito caducis instructus; receptaculum eglandulosum; calyx valvatus, tubuliformi-campanulatus, 2-3-lobatus, ca 1.5 cm longus, extrinseccus in sicco nigrescens glaberque, intus praecipue in parte dimidia inferiore albido-sericeus, lobis depresse ovatis apiceque rotundatis; petala 5, anguste oblonga, basi leviter angustata et basi tubi staminei adnata, apice acuta, ca 6 cm longa et 1 cm lata, cremea sed marginibus rubellis, carnosa, marginibus integris quidem in sicco undulato-crispatis, utrinque praeter imam partem stellato-puberula ad dense stellato-tomentella; tubus stamineus usque ad 5.5 cm longus, praeter partem inferiorem incrassatam cylindrico-

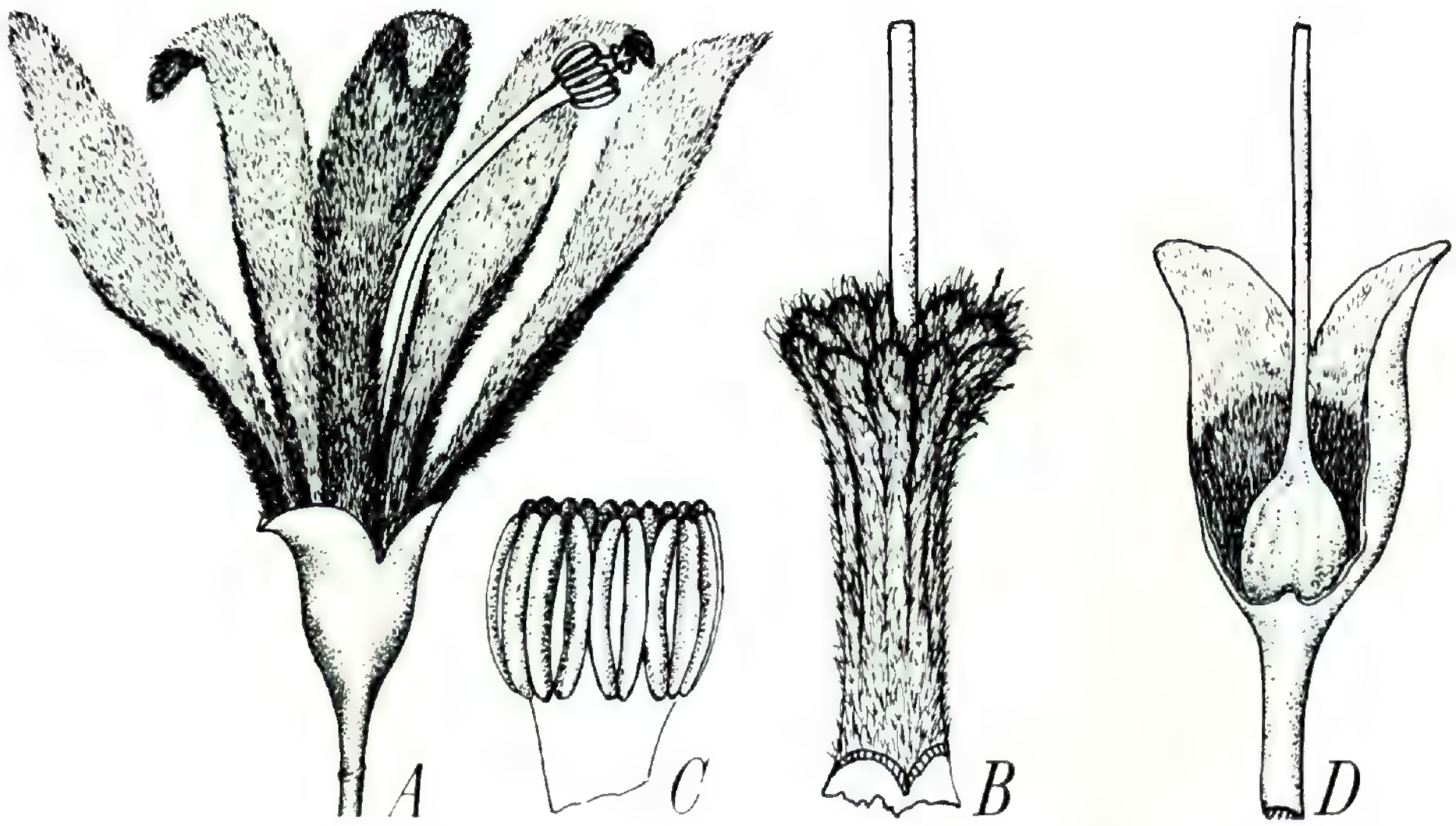

Fig. 1. *Chorisia incana* A. Robyns: A, flower (×1); B, lower part of staminal tube and verticil of antherless lobes (×4); C, apical part of staminal tube with anthers (×3); D, longitudinal section of calyx and ovary (×2). After *Belém & Magalhães 694*.

filiformis, leviter curvatus, in sicco nigrescens, glaber, apice leviter incrassatus et breviter 5-lobatus, parte inferiore incrassata ca 1 cm longa 3.5 mm diam longitudinaliter 10-sulcata dense stellato-incana apiceque verticillo loborum sine antheris (annulo staminodiorum?) cincta, lobis 5 crassis bipartitis ca 3 mm longis dense stellato-incanis indumentoque paucis pilis simplicibus longioribus et glandulosis immixto; antherae 5 dithecae, apice tubi staminei adnatae, thecis extrorsis ± linearibus parallelis ca 5 mm longis longitudinaliterque dehiscentibus; ovarium plus minusve globosum, ca 4-5 mm diam, glaberrimum et in sicco nigriscens, 5-loculare; stylus filiformis, tubo stamineo leviter longior et glaber, stigmate 5-lobato. *Capsula* ignota.

BRAZIL. BAHÍA: Rodovia Itabuna - Ilhéus, Beira da estrada, Apr 1965, *Belém & Magalhães 694* (holotype BR, isotype MO).

Quararibea **dolichopoda** A. Robyns, sp. nov.

Arbor parva, ramulis novellis densissime minutissimeque stellato-tomentellis mox glabrescentibus. *Folia* alternata, simplicia, petiolata petioloque 2-3.5 cm longo tereti basi apiceque leviter pulvinato densissime minutissimeque stellato-tomentello; lamina leviter inaequilateralis, anguste elliptica, basi subobliqua et rotundata ad obtusa, apice longe acuminata, usque ad 31 cm longa et 10 cm lata, chartacea, marginibus integris, utrinque praeter nervos parum minute stellato-puberulos et inconspicue rufidulo-lepidotos glabra, basi 3- vel obsolete 5-nervia, nervo mediano et nervis secundariis supra fere prominulis subtusque prominentibus. *Flores* oppositifolii, solitarii; pedicellus fructifer elongatus, ± flexuosus, teres, apicem versus

sensim dilatatus, 7-9 cm longus, densissime minutissimeque stellato-ferrugineo-tomentellus sed basin versus glabrescens, ut videtur ebracteolatus; calyx verisimiliter accrescens (vel tantum persistens?), in statu fructifero cupulatus, irregulariter lobatus, ca 2.5 cm longus et 3 cm latus, extus scabridulo-granulatus et dense minutissimeque stellato-ferrugineo-tomentellus, intus praecipue apicem versus dense ferrugineo-sericeus. *Capsula* drupacea, ± transverse late elliptica, apice emarginata et mucronata (styli basi persistenti), ca 2.2 cm longa et 3 cm diam, pericarpio fibroso extrinsecus minute scabridulo-granulato et dense minuteque stellato-ferrugineo-tomentello, 5-locularis loculisque 1-seminalibus; semina ut videtur angulata et ca 1 cm longa.

Panama. panama: halfway betw Goofy Lake & Cerro Jefe, in forest understory, April 27, 1966, *Blum, Duke & Odum 2274* (holotype MO).

Quararibea dolichopoda can readily be distinguished from the other six species of *Quararibea* occuring in Panama (cf. A. Robyns, Ann. Missouri Bot. Gard. **51:** 54-62, 1964) by a combination of the following characters: leaf blades very slightly inequilateral and 3- or obsoletely 5-nerved from the base; pedicels elongate, more or less flexuose, up to 7-9 cm long and apparently ebracteolate; capsule transversely broadly elliptic, emarginate and mucronate at the apex, 5-celled.—*André Robyns, Missouri Botanical Garden, St. Louis, Missouri & National Foundation for Scientific Research, Belgium.*

A NEW SPECIES OF RINOREA (VIOLACEAE) FROM PANAMA

Rinorea **dasyadena** A. Robyns, sp. nov.; ab affini *R. squamata* Blake ramulis et foliis statu juvenili pilosis sed mox glabris, lamina inaequilaterali basique obliqua hinc rotundata illinc obtusa ad acuta, petalis brevioribus et 3.5-3.8 mm longis, staminum filamentorum glandulis filamentis ca dimidiore brevioribus pilosisque, placentis 2-ovulatis styloque etiam breviore et 1.5-1.8 mm longo valde recedit.—Fig. 1.

Arbor (?) ca 5 m alta, ramulis juvenilibus appresso-ferrugineo-pilosis sed mox glabris. *Folia* opposita breviter petiolata petiolisque usque ad 5 mm longis infra rotundatis supra canaliculatis juventute appresso-ferrugineo-pilosis sed mox glabris, stipulis celeriter caducis; lamina inaequilateralis, elliptica, basi obliqua hinc rotundata illinc obtusa ad acuta, apice longe acuminata, usque ad 13.5 cm longa et 5 cm lata, membranaceo-chartacea, marginibus integris, juventute supra praecipue in costa minute puberula et infra sparse ferrugineo-appresso-pilosa, celeriter glabra, nervo mediano supra carinato infraque prominenti. *Inflorescentiae* racemosae, subterminales, rachidi usque ad 4 cm longa sparseque appresso-pilosula, pedicellis prope basin articulatis usque ad 2.5 mm longis et praecipue infra articulationem sparse appresso-puberulis, bracteis atque bracteolis pedicellis brevioribus celeriterque caducis. *Flores* sepalis subaequantibus latissime ovatis apice acutis ca 1 mm longis et latis tenuiter minuteque ciliolatis; petala ovata, apice obtusa ad rotundata et recurvata, 3.5-3.8 mm longa et 1.3-1.5 mm lata, marginibus tenuiter et minute

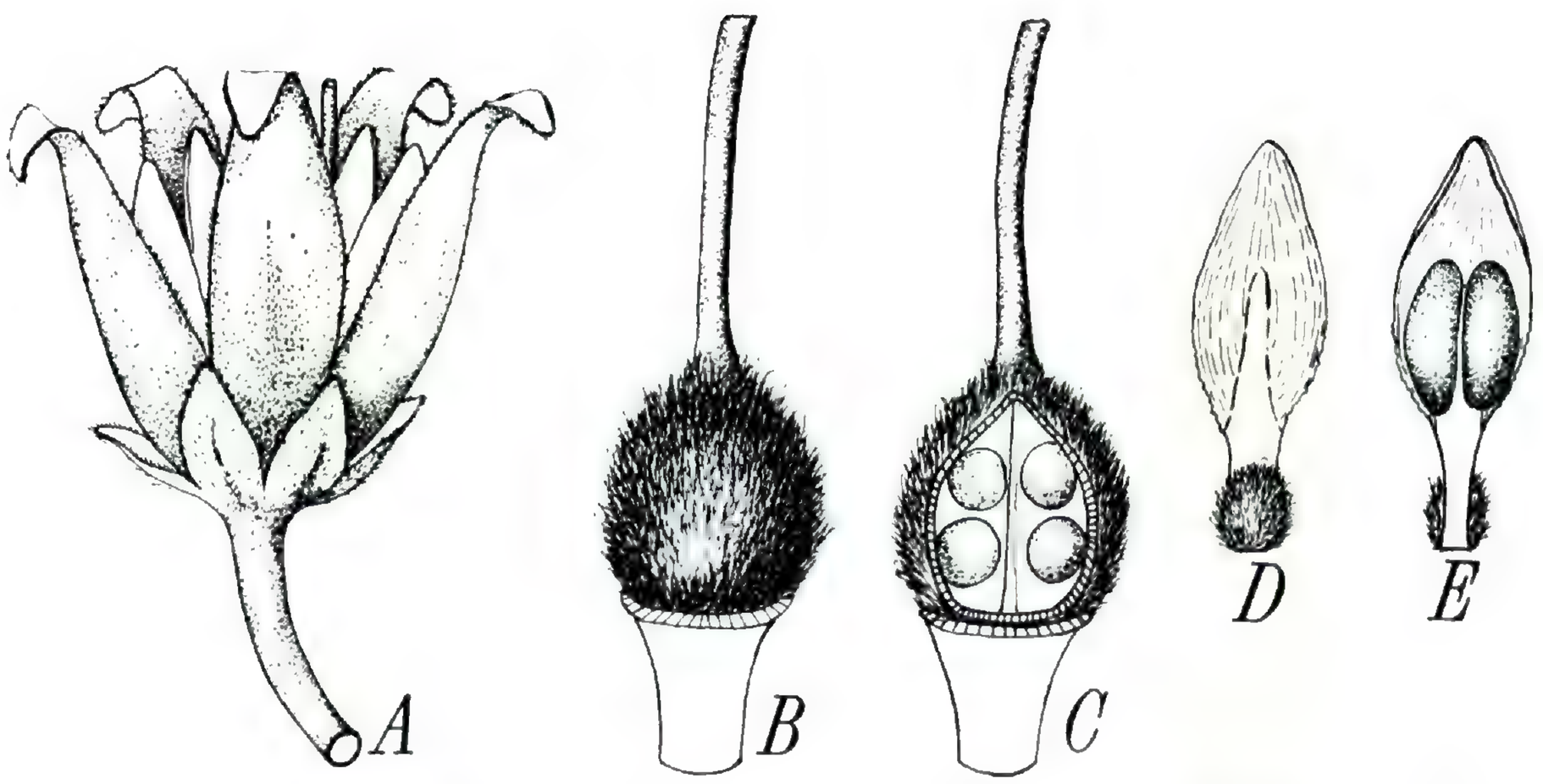

Fig. 1. *Rinorea dasyadena* A. Robyns: A, flower (×10); B, gynoecium (×15); C, longitudinal section of ovary and style (×15); D, stamen, abaxial view (×12); E, id., adaxial view (×12). After *Blum, Duke & Odum 2273.*

ciliolatis; stamina filamentis ca 0.8 mm longis dorsaliter glandulosis glandulisque filamentis ca dimidio brevioribus et pilosis, antheris ca 1 mm longis, connectivo a basi in squamas fuscas scariosas ovatas apice rotundatas praecipue basin versus erosulosas ca 1.8 mm longas et 1 mm latas et thecas 0.8-1 mm superantes dilatato; ovarium late ovoideum, ca 1 mm longum et latum, dense appresso-hispidum, placentis 3 2-ovulatis ovulisque superpositis, stylo 1.5-1.8 mm longo et glabro vel imo basi hispido, stigmate terminali. *Capsula* ignota.

PANAMA. PANAMA: halfway betw Goofy Lake & Cerro Jefe, in forest understory, April 27, 1966, *Odum* 2273 (holotype MO).

Rinorea dasyadena can be inserted in the specific key of the genus *Rinorea* in the revision of the *Violaceae* of the Flora of Panama (Ann. Missouri Bot. Gard. **54:** 66-67, 1967) as follows:

a. Leaves opposite; inflorescences racemose; connective dilated dorsally from the base into brownish scales.
  b. Bracteoles exceeding the pedicels; sepals 3-4.5 mm long; petals slightly longer than the sepals; filaments without dorsal glandular appendages; leaf blades oblique and rounded to slightly cordate at the base .....1. *R. sylvatica*
  bb. Bracteoles shorter than the pedicels; sepals 1-2.5 mm long; petals twice as long as the sepals or longer; filaments with a dorsal glandular appendage.
    c. Sepals 1-1.6 mm long; filaments ca 0.8-1 mm long; anthers with the thecae unappendaged; leaf blades membranous-chartaceous to chartaceous.
      * Glandular appendages of the filaments about as long as or slightly shorter than the filaments, glabrous; placentae 1-ovulate; style ca 2.5 mm long; leaf blades usually slightly oblique and acute to obtuse at the base; branchlets and leaves ferruginous-puberulous and sparsely hirsute .....2. *R. squamata*

** Glandular appendages of the filaments about ½ as long as the filaments, pilose; placentae 2-ovulate; style ca 1.5-1.8 mm long; leaf blades oblique at the base, rounded on one side and obtuse to acute on the other side; branchlets and leaves pilose when young, but soon glabrous .....2a. *R. dasyadena*

cc. Sepals 2-2.5 mm long; filaments scarcely 0.4 mm long, the glandular appendages about as long as the filaments, glabrous; anthers with the thecae mucronate; leaf blades slightly inequilateral or not, narrowly ovate, acute to obtuse at the base .....3. *R. brachythrix*

aa. Leaves alternate; inflorescences etc.

—*André Robyns, Missouri Botanical Garden, St. Louis, Missouri & National Foundation for Scientific Research, Belgium.*

VOCHYSIA JEFENSIS A. ROBYNS, SP. NOV. (VOCHYSIACEAE)

Since the publication of the *Vochysiaceae* for the Flora of Panama (Ann. Missouri Bot. Gard. **54:** 1-7, 1967) a recent collection of *Vochysia* collected at the top of Cerro Jefe in the Province of Panama was received at the herbarium. This collection represents a new species of *Vochysia* belonging to the sect. *Ciliantha* Stafleu. It can be readily distinguished from the two species of *Vochysia* occurring in Panama (*V. ferruginea* Mart., and *V. hondurensis* Sprague) by the corolla reduced to only one petal.

Vochysia **jefensis** A. Robyns, sp. nov.—Fig. 1.

Frutex ramulis quadrangularibus glabris et haud decorticantibus. *Folia* opposita, stipulis minutissimis ca 1 mm longis deltoideis persistentibusque; petiolus usque ad 12 mm longus, supra canaliculatus glaberque; lamina elliptica ad plus minusve obovato-elliptica, basi acuminata leviterque decurrens, apice rotundata vel rotundato-mammillata saepeque subretusa, usque ad 8.5 cm longa et 5.2 cm lata, rigide chartacea ad subcoriacea, marginibus planis ad subrecurvatis, utrinque glabra surdaque, supra (in sicco) leviter pallidiora, nervo mediano supra leviter immerso subtusque valde prominenti, nervis secundariis ca 12 utrinque haud prominentibus, costa marginale nulla. *Inflorescentiae* terminales, densiflores, contracti et usque ad 4 cm longae, cincinnis 1-2-floris, rachidi atque pedunculis pedicellisque glabris quadrangularibus. *Flores* sulphurei, oblique zygomorphi, usque ad 24 mm longi; calyx lobo calcarato carnoso glabro 12-16 mm longo (sine calcari), calcari cylindrico basi rotundato parum incurvato ad fere recto lobo ca dimidio breviore vel minore (5-8 mm longo), ceteris lobis late ovatis acutis ad ± obtusis 1.5-3 mm longis et 1.5-2 mm latis marginibus tenuiter ciliolatis glabrisque; petalum unicum, ellipticum, marginibus plus minusve erosulosis, usque ad 5 mm longum et 2.25 mm latum, tenuiter ciliatum, dorso praesertim in parte dimidia inferiore appresso-piloso; stamen unicum, subclavatum, usque ad 14 mm longum, connectivo basin versus sensim in filamentum breve 1-3 mm longum attenuato marginibus ciliatis et in parte adaxiali sterili basali interque thecas piloso, thecis 2 introrsis disjunctis 6-7 mm longis connectivi apice cucullato ca 1 mm longo

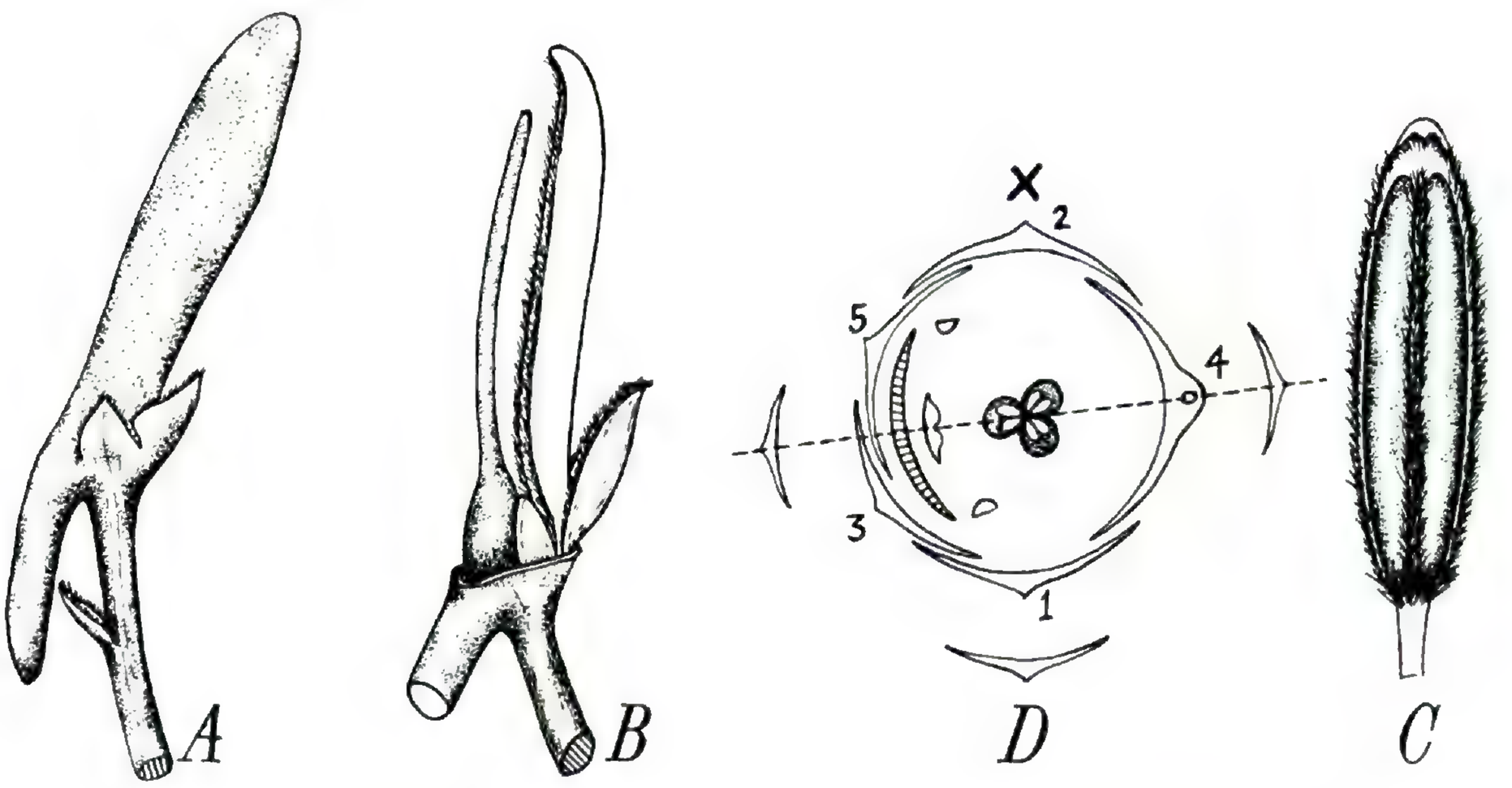

Fig. 1. *Vochysia jefensis* A. Robyns: A, flower bud (×3); B, flower, calyx removed (×4); C, stamen, adaxial view (×5); D, floral diagram. After *Dwyer, Gauger & Baker 7269*.

coronatis longitudinaliter dehiscentibus; staminodia 2, parvula, deltoidea, eciliata, usque ad 1.5 mm longa; ovarium ca 2 mm longum, glabrum, stylo cylindrico leviter curvato 7-13 mm longo glabroque, stigmate terminali truncatoque. *Capsula* ignota.

PANAMA. PANAMA: Cerro Jefe, summit, alt 2900 ft, March 12, 1967, *Dwyer, Gauger & Baker 7269* (holotype MO).

The following is a new key to the three species of *Vochysia* from Panama:

a. Leaves opposite.
   b. Spur strongly recurved, about as long as the lobe; petals 3, 9-10 mm long; branchlets, lower surface of the leaf blades, and inflorescence axes ferruginous-tomentellous or ferruginous-puberulous; leaf blades acuminate to caudate-acuminate at the apex, the acumen to 15 mm long .....*V. ferruginea*
   bb. Spur slightly incurved to almost straight, ca ½ as long as the lobe or less; petal 1, to 5 mm long; branchlets and leaves glabrous; inflorescence axes glabrous to sparsely and minutely pilose; leaf blades with the apex rounded to rounded-mammillate and often subretuse .....*V. jefensis*

aa. Leaves 3-4-verticillate; spur straight or only slightly curved, ca ½-⅔ as long as the blade; petals 3, ca 4-5 mm long; branchlets, lower surface of the leaf blades and inflorescence axes glabrous or sparsely puberulous; leaf blades rounded or obtuse and usually ± retuse at the apex .....*V. hondurensis*

—*André Robyns, Missouri Botanical Garden, St. Louis, Missouri & National Foundation for Scientific Research, Belgium.*

LAETIA MICRANTHA A. ROBYNS, A NEW SPECIES OF FLACOURTIACEAE FROM PANAMA

Up to now only one species of *Laetia* Loefl. ex L. was reported from Panama as well as from North America. The revision of the *Flacourtiaceae* for the Flora of Panama has turned up three species for that country, i.e. *L. thamnia* L. (southern Mexico, Central America, Colombia, and the West Indies), *L. procera* (Poepp. & Endl.) Eich. (Panama, Guyanas, and northern Brazil), and a new species, *L. micrantha.* This new taxon is found in the Province of Darien and belongs to the sect. *Casinga* Warb. (see Gilg in Engl., Nat. Pflanzenfam. ed. 2, **21:** 448, 1925). It is characterized by the minute flowers, hence the specific epithet *micrantha.*

Laetia **micrantha** A. Robyns, sp. nov.

Arbor 18-20 m alta, trunco 12.5-25 cm diam, ligno duro, ramulis puberulis. *Folia* alterna, disticha, in ramulis pendula, petiolis 5 mm longis et puberulo-villosis, stipulis anguste triangularibus ca 4 mm longis et basi 1 mm latis fugacibusque; lamina anguste ovato-oblonga ad anguste oblonga, basi subobliqua ad manifeste oblique et hinc obtusa ad rotundata illinc acuta ad obtusa, apice longe acuminata acumineque gracili, marginibus serrulatis, 6-13 cm longa et 1.5-4.5 cm lata, membranacea ad tenuiter chartacea, dense pellucido-punctata, praecipue supra ± nitida, utrinque minute puberula, costa infra prominenti, venis lateralibus infra prominulis. *Inflorescentiae* axillares, dense fasciculatae, bracteis numerosis parvis liberis ca 1 mm longis persistentibus et in axillis foliorum pulvinos formantibus. *Flores* hermaphroditi, albidi, parvuli et usque ad 2 mm longi, pedicellis filiformibus usque ad 4 mm longis ca 1 mm supra basin articulatis minuteque puberulis; sepala 5, imbricata, libera vel fere libera, ± obovata, leviter cucullata, apice rotundata, ca 1.8-2 mm longa et 1-1.3 mm lata, membranacea, sub anthesi erecta, extrinsecus minute puberula; petala nulla; stamina 10, vix perigyna, uniseriata, exserta, filamentibus filiformibus subaequalibus 2-2.5 mm longis glabrisque, antheris introrsis ca 0.3 mm longis et longitudinaliter dehiscentibus; ovarium subglobosum, ca 0.7-0.8 mm diam, glabrum, 1-loculatum, placentis 3 parietalibus 2-ovulatis, stylo ca 1.3 mm longo apice breviter sed distincte 3-fido ramisque 0.2 mm longis, stigmatibus 3 leviter dilatatis. *Fructus* ignotus.

PANAMA. DARIEN: Río Perrecenico, *Duke & Bristan* 238 (MO); trail betw Paya & Palo de las Letras, *Stern et al. 206* (US); vic of Caná, alt 1750 ft, hillside, in dense wood, *Stern, Chambers, Dwyer, Ebinger 513* (holotype MO, isotype US).

According to Duke & Bristan this species is called colloquially *raspalengua;* they also report that the fruit is edible and that the wood may be used for firewood when dry.—*André Robyns, Missouri Botanical Garden, St. Louis, Missouri & National Foundation for Scientific Research, Belgium.*

ACIDOTON (EUPHORBIACEAE) IN CENTRAL AMERICA

Acidoton **nicaraguensis** (Hemsl.) Webster, comb, nov.

Cleidion ? nicaraguense Hemsl., Biol. Centr.-Amer. **3:** 130, 1883.
Gitara panamensis Croizat, Jour. Arnold Arb. **26:** 192, 1945.

As treated in the last monographic revision by Pax & Hoffmann (Pflanzenr. **IV,** 147, IX (Heft 68): 24-26, 1919), *Acidoton* is a small West Indian genus of two species. A few years after that treatment, Pax & Hoffmann described a new genus *Gitara* (Pflanzenr. **IV,** 147, XVII (Heft 85): 187, 1924) on the basis of a Venezuelan plant, and noted that it was very close to *Tragia.* Finally, Croizat (Jour. Arnold Arb. **26:** 192, 1945) described *Gitara panamensis* on the basis of a specimen from Panama (Darien, betw Pinogana & Yavisa, *Pittier 6543;* holotype A; isotype US). He was correct in seeing an affinity between the Panamanian plant and *Gitara venezolana,* but neither he nor Pax & Hoffmann seems to have noticed a possible resemblance with *Acidoton.*

Recently, in attempting to fix the identity of *Cleidion ? nicaraguense* Hemsl., I found that the type specimen of *Gitara panamensis* Croizat agreed closely with Hemsley's description, as well as a specimen from Nicaragua (*Engelsing s.n.,* NY). Although I have not been able to examine Hemsley's types (Nicaragua, Chontales, *Tate 352, 455;* presumably at K), there can be little doubt that we are dealing with a single species which ranges from Nicaragua to Panama.

The Central American species of *Acidoton* resembles the West Indian ones in having a large number of stamens (24-35), axillary inflorescences, and stinging hairs present on various organs. The apical tuft of small stinging hairs on the anthers is very similar in all of the species, and furnishes a good diagnostic character to distinguish *Acidoton* from *Tragia.* There can be no doubt that *Acidoton* is very close to *Tragia,* as suggested by Pax & Hoffmann when they proposed *Gitara.* However, the apically tufted anthers and large number of stamens clearly set *Acidoton* apart from most species of *Tragia.* One Mexican species, *T. bailloniana* Muell. Arg., which was made the basis for the genus *Zuckertia* by Baillon does agree with *Acidoton* in its large stamen number and apiculate anthers. For the present, it seems best to leave it in *Tragia* because of its climbing habit, but its status may well be subject to reevaluation.

The relationship between the Central American and Venezuelan taxa of *Acidoton* remains to be elucidated. They are doubtless closely related, and might possibly prove to be races of a single wide-ranging species. However, the differences in leaf shape and venation pointed out by Croizat appear to be sufficient to justify maintaining (*ad interim*) the Venezuelan taxon as a direct species:
Acidoton **venezolanus** (Pax & Hoffm.) Webster, comb. nov.

Gitara venezolana Pax & Hoffm., Pflanzenr. **IV,** 147, XVII (Heft 85): 187, 1924.

As thus construed, *Acidoton* is now a Caribbean genus with six species: 3 in Hispaniola, 1 in Jamaica, 1 in Central America, and 1 in northern South America.
—*Grady Webster, University of California, Davis.*

A NEW SPECIES OF CAPERONIA (EUPHORBIACEAE) FROM PANAMA[1]

Caperonia **neglecta** Webster, sp. nov. (section *Caperonia*).

Annua, monoica, ca 2-5 dm alta; caulis inermis, ramosus, petiolis et foliis atque setulis glanduligeris atque trichomatibus hispidulis vestitis. *Folia* petiolata petiolisque 1.5-5 mm longis; stipulae lanceolatae, ciliatae, ca 1.5-4.5 mm longae; lamina plerumque elliptica, acuta, membranacea, ca 3-7 cm longa, 1-3 cm lata, basi obtusa vel rotundata, nervis secundariis rectis, margine serrulato. *Racemi* 1.5-3 cm longi, inferne 1-3 flores ♀ gerentes, ceterum flores ♂; bracteae hispidulo-ciliatae. *Flos* ♂: laciniae calycis 5, inaequales, sparsim hispidulae; petala 5, manifeste inaequalia, longiora 3 ca 1.5-1.8 mm longa; stamina 10, biverticellata, antheris 0.3-0.4 mm longis; ovarii rudimentum rotundatum, ca 0.25-0.3 mm longum. *Flos* ♀: pedicellus hispidulus, 2.4-2.7 mm longus; laciniae calycis 5, subaequales, glanduligerae hispidulaeque, ca 1.5-2.2 mm longae; petala 5, sub-aequalia, exserta, anguste elliptica, 1.2-1.6 mm longa; ovarium hispidulum et glandulis fusiformibus vestitum; styli ca 1 mm longi, profunde 3-lobati. *Capsulae* 4.5-5.5 mm latae; semina fusca, 2.3-2.7 mm diam.

PANAMA. PANAMA: Camino del Boticario, nr Chepo, *Pittier 4545* (holotype US); Tumba Muerto Rd. nr Panama City, *Standley 29769* (US), *29815* (US).

This nondescript and apparently weedy species has remained undescribed for several years in the vain hope that a name could be found for it. The type collection was annotated by Käthe Hoffmann as *Caperonia palustris* (L.) St.-Hil.; and indeed all of the specimens have been misdetermined as that species. The plant does have a considerable superficial resemblance to *C. palustris,* due to its copious glandular pubescence and many-toothed leaf blades. However, it is sharply distinguished from that species by its pedicellate ribbed pistillate calyx, unequal male petals, entire pistillode, and hispidulous ovary. In some respects such as the hispidulous ovary and short inflorescence it resembles *C. paludosa* Kl., but it differs in its elongated stipules, copious glandular pubescence, and pedicellate pistillate flower. In some ways *C. neglecta* shows more resemblance to various African species such as *C. hirtella* Beille, but seems to differ from all of these in the combination of a pedicellate pistillate flower with 3-lobed styles and lanceolate stipules. The apparent restriction of *C. neglecta* to weedy habitats, together with its sporadic occurrence, suggests the possibility of its being a comparatively recent introduction; but if so, the original population in Africa appears not to have been detected thus far.—*Grady Webster, University of California, Davis.*

[1] I wish to acknowledge the generous assistance of Dr. A. Robyns in the preparation of the Latin descriptions.

TWO NEOTROPICAL TAXA OF DALECHAMPIA (EUPHORBIACEAE)

1. *Dalechampia* **hutchinsoniana** Webster, sp. nov.

Frutex 1.5 m altus, ramis stramineis laevibus. *Folia* simplicia, glabrata, elliptica vel oblonga, argute serrulata, apiculata, ca 1.5-3 cm longa, 0.5-1 cm lata, ad basin quintuplinervia, petiolis 1-3 mm longis; stipulae lanceolatae, acuminatae, 2.5-6 mm longae, striato-costatae. *Inflorescentiae* solitariae, pseudo-axillares, pedunculis glabratis ca 3-6 cm longis; bracteae involucrales obovatae, atro-sanguineae, glabratae, quintuplinerviae, lacerato-dentatae, unguiculatae, ca 2-2.5 cm longae, 1 cm latae, stipellis lanceolatis 4-7 mm longis; bracteae cymae ♀ scariosae, minute hispidulae, ca 2.5 mm longae; bracteae pleiochasii primariae 4, subrotundatae vel oblongae, concavae, evidenter glabratae (minutissime hispidulae), multinervosae, ca 3.5-4 mm longae, 3.5-6 mm latae, ± liberae; nectarium ca 5-6 mm latum, e bracteolis tenuibus fimbriatis pluribus compositum. *Flores* ♂ ca 9 in quoque pleiochasio, pedicellis ad 3 mm longis; laciniae calycis saepe 4, oblongo-lanceolatae, minute hispidulae, 2.5-3 mm longae; columna staminalis cylindrica, dense hispidula, 2-2.3 mm longa, antheris 24-28, ca 0.5-0.6 mm longis. *Flores* ♀ 3, pedicellis ca 1.5 mm longis; laciniae calycis 7-9, lineari-lanceolatae, ca 4-6 mm longae, pinnatifido-laciniatae, laciniis glandulosis, glandulis intersepalis paucis ca 0.2 mm longis; ovarium fere 1 mm longum, dense hispidulum; columna stylaris ca 3.5-4 mm longa, 0.5-0.6 mm lata, minute hispidula, stigmate dilatato-emarginato 1.2-1.3 mm diam. *Capsulae* ut semina ignotae.

PERU. PROV CELENDIN: Dept Cajamarca, cliffs below bridge, Río Marañon opposite Balsas, 800 m, 30 May 1964, *Hutchinson & Wright 5446* (holotype MO; isotypes DAV, UC).

This striking species, which appears to be endemic to a restricted region in northern Peru, is not closely related to any other. The shrubby stems, simple palmatinerved leaves, and pinnately lobed sepals suggest a relationship to sect. *Humiles* Pax & Hoffm. (Pflanzenr. **IV,** 147, XII: 53, 1919). However, the dark reddish unguiculate involucral bracts and larger stamen number immediately distinguish it from any species in that section. The bracts and androecium of *D. hutchinsoniana* to some extent resemble those found in species of sect. *Dioscoreifoliae* Pax & Hoffm., but all of those plants are twining vines. Probably this Peruvian species will have to be placed in a new supraspecific taxon.

2. *Dalechampia cissifolia* Poepp. & Endl. subsp. **panamensis** (Pax & Hoffm.) Webster, stat. nov.

Dalechampia panamensis Pax & Hoffm., Pflanzenr. **IV,** 147, XII (Heft 68): 19, 1919.

The taxonomic identity of the only Panamanian *Dalechampia* with compound leaves has remained rather uncertain up to the present. Mueller (Prodr. **15**(2): 1241, 1866) based his *D. stenosepala* on a Brazilian collection of Sello as well as one from Costa Rica (mistakenly ascribed to Panama by Mueller: 'inter Jose et

Puntarenas', *Oersted;* B, n.v.). Pax & Hoffmann (loc. cit.) restricted the name *D. stenosepala* to the Brazilian plant and separated the Central American plant as *D. panamensis.*

In their treatment of the species in sect. *Triphyllae,* Pax & Hoffmann placed *D. panamensis* adjacent to *D. cissifolia,* with which it is indubitably closely related. The leaf characters given in their key are most unconvincing as the Panama plants often have distinctly dentate rather than 'subentire' leaflets. The only characteristics in which Peruvian specimens of *D. cissifolia* appear to differ significantly include longer fruiting pedicels (up to 4 cm long) and calyx-lobes (up to 1.5 cm long as compared to 1 cm for Panamanian specimens).

It seems most reasonable to treat the Central American representatives of this complex as a subspecies of *D. cissifolia;* the South American plants would then fall into subsp. *cissifolia.* It is probable that *D. stenosepala* should also be included in *D. cissifolia,* but until critical comparisons are made no change in its status is suggested.—*Grady Webster, University of California, Davis.*

A REMARKABLE NEW PHYLLANTHUS (EUPHORBIACEAE) FROM CENTRAL AMERICA

During the preparation of a synopsis of the American taxa of *Phyllanthus* (Webster, ined.), it has proven necessary to describe a number of novelties. Among these is a Central American plant which occupies such an isolated position that it deserves special treatment. Although most of the New World species of *Phyllanthus* can be fitted into the classification proposed for the West Indian ones (Webster, Jour. Arnold Arb. **37-39,** 1956-58), there are certain species which definitely do not belong to any of the previously established taxa; these, of course, are the most interesting ones.

The great majority of the woody species of American *Phyllanthus* belong to two subgenera with areolate pollen: *Botryanthus* and *Xylophylla.* However, others belong to the strictly American subg. *Conami,* and a few seem best classified in either the woody subgenera *Kirganelia* and *Emblica*[1] or the mainly herbaceous subg. *Phyllanthus.* The South American species include a number of aberrant taxa which will be given detailed treatment later. In contrast, only a single North American species—the one described below—cannot easily fit into the subgeneric taxa already established. It, therefore, is necessary to create a new section for the species at the same time that it is formally described.

Phyllanthus section **Calodictyon,** sect. nov.

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[1] *Phyllanthus* subg. **Emblica** (*Gaertn.*) Webster, stat. nov., based on *Emblica* Gaertn., Fruct. Sem. **2:** 122, 1790.

Arbuscula monoica, glabra, ramificatione more sectionis *Phyllanthi;* cataphyllae induratae, deciduae; folia magna, chartacea, prominenter reticulata; cymulae axillares, bisexuales; flores calycis laciniis 5, disco ♂ segmentis 3 duplicibus, disco ♀ 5-angulato, staminibus 3, liberis, antheris muticis verticaliter dehiscentibus, granis pollinis subglobosis tricolporatis tectatis perreticulatis, ovario loculis 3, stylis bifidis alte connatis.

Type species: *Phyllanthus tuerckheimii* Webster. The name of the section alludes to the attractive reticulate-veined leaves.

Phyllanthus **tuerckheimii** Webster, sp. nov.—Fig.1.

Arbuscula monoica, glabra, ramis subteretibus laevibus; cataphylla indurata, brunnea, evidenter decidua, stipulis triangularibus ca 3.5-4 mm longis, crassiusculis, lamina lanceolata; ramuli 12-20 cm longi, 2.2-3 mm diam, subcomplanati angulative, plumbei, laeves, cum foliis 5-10; internodium proximale 2-6 cm; internodia mediana plerumque 1-3 cm longa. *Folia* stipulis brunneis, induratis,

Fig. 1. *Phyllanthus tuerckheimii* Webster: deciduous branchlet, ×1/3 (*Tuerckheim 1085*).

subpersistentibus, lanceolatis, ca 3-4 mm longis; petioli 3-4 mm longi; laminae chartaceae, ± ellipticae, plerumque 7-14 cm longae, 2.5-5 cm latae, abrupte acutae vel acuminatae, utrinque olivaceae et lucidae, venis venulisque prominenter reticulatis, marginibus planis. *Inflorescentiae* cymosae, cymulis bisexualibus in ramulis axillaribus; cymulae cum floribus pluribus, 2-4 ad eundum nodum. *Flores* ♂ pedicellis tenibus 5-9 mm longis; laciniae calycis 5, subaequalae, ellipticae vel obovatae, integrae, obtusae, ca 2.5-4 mm longae, 1.5-2.2 mm latae; discus ca 1.5-2.2 mm latus, segmentis 3 bilobis crassis et foveatis; stamina 3, filamentis liberis 0.6-1.0 mm longis, antheris ovatis oblongisve obtusis 0.6-0.7 mm longis verticaliter dehiscentibus; pollinis grana subglobosa, tricolporata, colpibus ad polos convenientibus, exinio crasso perreticulato. *Flores* ♀ pedicellis crassiusculis 6-9 mm longis; laciniae calycis 5, subaequalae, ± erectae, ellipticae vel obovatae, 4-5.5 mm longae, 2.5-4 mm latae, reticulate nervatae; discus crateriformis, 5-angulatus, crassiusculus, prominenter foveatus, 2-3 mm latus, 0.6-0.8 mm altus; ovarium laeve; styli connati, columna 2.5-3 mm alta, apicibus bifidis vel bipartitis 0.9-1.2 mm longis gracilibus et patentibus. *Fructus* seminaque ignoti.

Type: Guatemala, Alta Verapaz, Pansamalá, alt 3800 ft, Sept 1886, *von Tuerckheim 1085* (holotype, US 931347; isotypes, US, GH).

This species, known only from the type collection, was determined on the printed labels as *P. grandifolius* L., but this is a double error. The plant was evidently mistaken for *P. grandifolius* sensu Muell.-Arg. non L. (DC., Prodr. **15**(2): 329, 1866), which is the West Indian species correctly know as *P. juglandifolius* Willd. This latter plant, belonging to sect. *Asterandra* in subg. *Xylophylla*, does somewhat resemble the Guatemalan species under discussion in its large reticulate-veined leaves. The massive pitted floral disk in *P. juglandifolius* also recalls that in *P. tuerckheimii* (Fig. 2). However, *P. juglandifolius* is very different in its dilated style-tips, connate horizontally dehiscent stamens, and especially in its areolate pollen grains which are typical for subg. *Xylophylla* and utterly different from the tricolporate coarsely reticulate grains of *P. tuerckheimii*. True *P. grandifolius* L., which does occur in Guatemala, is even more different in its non-phyllanthoid branching and elaborately ramified inflorescences.

The overall configuration of the flowers in sect. *Calodictyon* would place the taxon in subg. *Gomphidium* (Baill.) Webster, a mainly Australasian group of species which approach the genus *Glochidion* in many respects. The ♂ flowers of *P. tuerckheimii*, with three free vertically dehiscent stamens and a disk of three massive duplex segments, definitely resemble those of various species of sect. *Gomphidium* from New Caledonia and New Guinea; the ♀ flowers, with a crateriform disk and bifid styles, suggest those found in New Guinean species of sect. *Paragomphidium* such as *P. finschii* K. Schum. (except that in the Guatemalan plant the styles are connate). The leaves are much like those of *P. brassii* White, from Queensland, but that species has dimerous ♂ flowers (4 calyx-lobes and 2 stamens) and free styles. Although the pollen grains of most taxa of subg. *Gomphidium* are similar to those of sect. *Calodictyon* in being tricolporate with colpi meeting at the poles, the unbordered colpi and coarse reticulum of the Guatemalan plant are not matched in any of them.

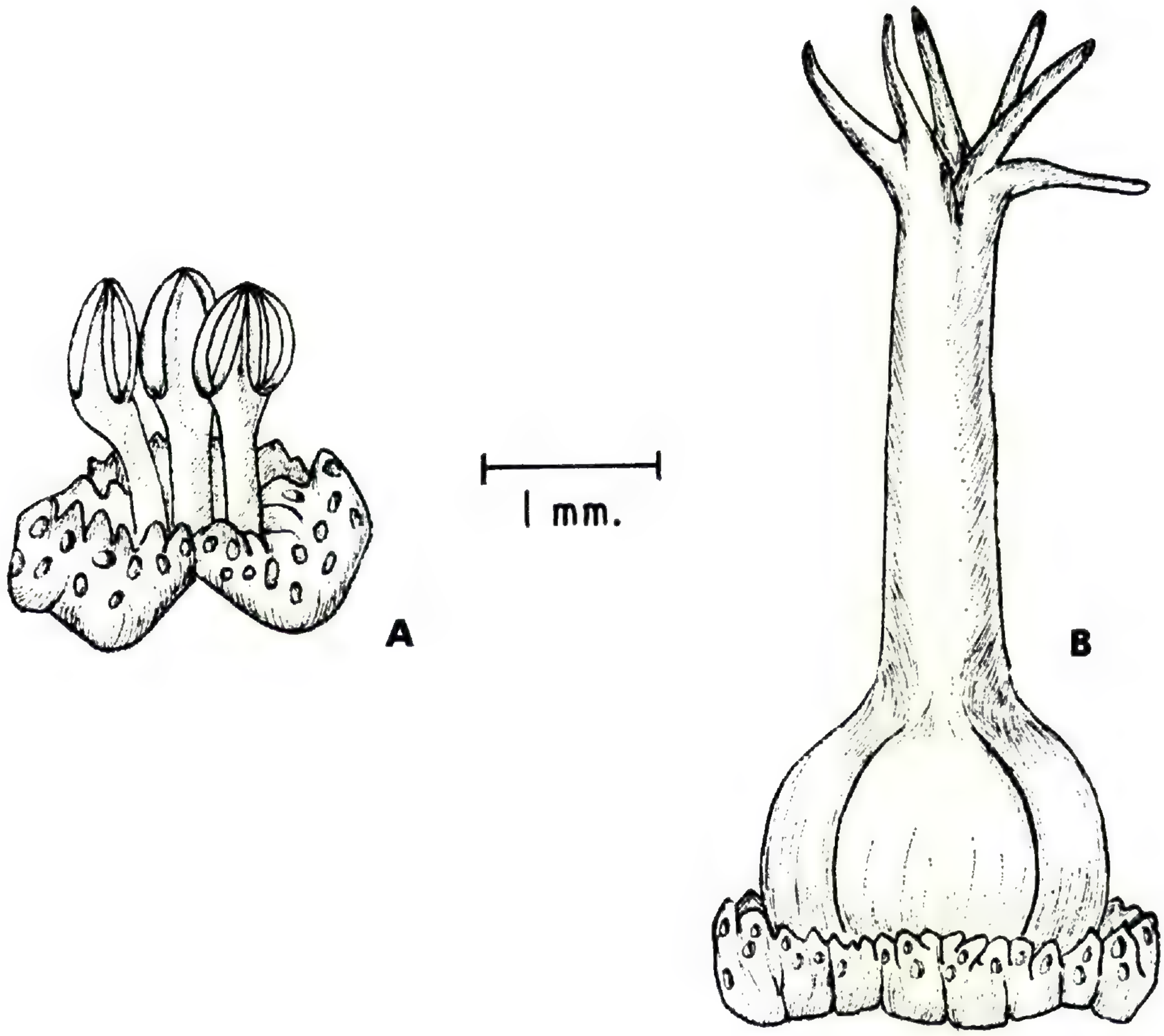

Fig. 2. *Phyllanthus tuerckheimii* Webster: A, androecium and disk of staminate flower; B, gynoecium and disk of pistillate flower. After *Tuerckheim 1085.*

On the basis of the totality of characters observed, the similarities of sect. *Calodictyon* with the taxa of subg. *Gomphidium* are so striking that the group apparently must be referred to that otherwise strictly gerontogean subgenus. The only other American taxa of *Phyllanthus* which seem to show possible affinities to subg. *Gomphidium* are the South American species of sect. *Microglochidion.* These plants have an androecium even more Gomphidium-like in the apiculate anthers, and some species have entire styles. However, the 6- to 8-colporate pollen grains of sect. *Microglochidion* are very different from those found in sect. *Gomphidium,* and for this reason the South American species seem better placed in subg. *Emblica,* where similar pollen grains occur.

The placement of sect. *Calodictyon* within subg. *Gomphidium* admittedly creates a geographical anomaly, since the subgenus thus becomes one of the few euphorbiaceous taxa which shows an Australasian-Mesoamerican disjunction. However, somewhat similar patterns are exhibited, e.g. by *Sebastiania* (mostly New World but with 1 Fijian species) and *Stillingia* (American except for 2 In-

donesian species). The isolated position of sect. *Calodictyon* within subg. *Gomphidium* suggests that it is probably best regarded as a relict group which has persisted from a time when subg. *Gomphidium* and subg. *Emblica* were much better represented in the New World.—*Grady Webster, University of California, Davis.*

NOTES ON SOME AMERICAN SPECIES OF PHYLLANTHUS (EUPHORBIACEAE)

1. *Phyllanthus abnormis* Baill. var. **riograndensis,** var. nov. ab var. *abnormi* differt ramis et foliis semper dense viscido-scabridulis, glandulis ♀ reniformibus. Type: Texas, Starr Co, 3 mi W of Sullivan City, on sand in open scrub, 2 Apr 1941, *Lundell & Lundell 9891* (MICH).

This striking variant of *Phyllanthus abnormis* replaces the typical form of the species in the lower Rio Grande Valley (Hidalgo, Starr, and Webb counties), and probably occurs on the Mexican side, although it has not yet been collected there. The laterally expanded disk-segments in the pistillate flower are so characteristic that at first encounter the Rio Grande plant might appear to be a distinct speceies. However, there is some evidence of intergradation with the glabrous plants which have narrow disk-segments, so it seems best to record this population as simply a local variety.

2. *Phyllanthus longipes* Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 153, 1940, non *P. longipes* (Wight) Muell.-Arg., Linnaea **32:** 11, 1863. Type: British Honduras, El Cayo Distr, Vaca, 13 May 1938, *Gentle 2619* (holotype F; isotypes MICH, MO). This plant is obviously not a *Phyllanthus,* and seems to represent a distinct species in the genus *Gymnanthes.* It may, therefore, take the name *Gymnanthes* **belizensis** Webster, nom. nov. Although similar to *G. riparia* (Schlecht.) Kl. and *G. longipes* Muell.-Arg. of Mexico, it seems to be distinct by virtue of its rigid leaves combined with long very slender fruiting pedicels.

3. *Phyllanthus* **ventricosus** Webster, sp. nov. (subg. *Botryanthus*). *Frutex* monoicus, ca 3 m altus, ramis teretibus persistentibus, ramulis juvenilibus minute ferrugineo-puberulis sed mox glabris. *Folia* alterna, chartacea, elliptica, obtuse acuminata, glabra, ca 5-9 cm longa 3-4 cm lata, nervis lateralibus utroque latere ca 7-9 supra inconspicuis subtus prominulis reticulato-anastomosantibus, petiolis ca 1.5-2.5 mm longis, stipulis deltoido-lanceolatis 0.9-1.1 mm longis. *Flores* in cymulis axillaribus bisexualibus vel ♂; flos ♀ solitarius; flores ♂ multi (plus quam 25) in quaque cymula. *Flores* ♂ pedicellis tenuibus ca 5-9 mm longis; laciniae calycis 6 biseriatae, obovatae, integrae, 1.2-1.5 mm longae, 0.7-0.9 mm latae; discus poculiformis, crassiusculus, ca 0.3-0.4 mm altus, 1 mm latus; stamina 3, omnino coalita in columnam ventricosam umbonatam 0.8-0.9 mm altam; antherae ex apice columnae inclinatae, loculis sacciformibus ca 0.5-0.6 mm longis; pollinis grana areolata, areolis polybrochatis. *Flores* ♀ pedicellis sparse puberulis sed glabrescentibus, ca 4-9 mm longis; laciniae calycis 6 biseriatae, oblongae vel

obovatae, integrae, 1.3-1.8 mm longae, 0.6-0.9 mm latae; discus crateriformis ca 0.3-0.4 mm altus, 1.5-1.6 mm latus; ovarium triloculare, stylis liberis patentibus bifidis ca 0.5 mm longis ramis tenuibus. *Capsulae* (immaturae) laeves, castaneae, 7-8 mm longae; semina non vidi.

Type: Peru, Dept Loreto, Distr Iquitos, Rancho Indiana, overflowed creek, alt 110 m, *Mexia 6414* (holotype MO 1188471; isotypes GH, UC, US).

The type collection of this species had been determined by Standley as *Phyllanthus poeppigianus* Muell. Arg., which is indeed superficially similar in appearance. However, *P. poeppigianus* is dioecious and has clearly different flowers: although the ♂ flower is similar in having a cupulate disk, the stamens are only partially connate (¾ to ⅘ the filament lengths) into a slender column ca 1.5 mm high; and the ♀ flowers are easily distinguished by their entire styles. Still, the 6-merous calyces and areolate pollen grains are similar in both species, and *P. ventricosus* may reasonably be assigned a position in subg. *Botryanthus* (Webster, Jour. Arnold Arb. **38:** 49, 1958) not too far distant from *P. poeppigianus*.—*Grady Webster, University of California, Davis.*

A SECOND SPECIES OF TETRORCHIDIUM (EUPHORBIACEAE) REPORTED FROM PANAMA

Tetrorchidium gorgonae Croizat subsp. **robledoanum** (Cuatr.) Webster, stat. nov.

Tetrorchidium robledoanum Cuatr., Brittonia **9:** 81, 1957.

The first record of *Tetrorchidium* from Panama was established by Standley (Publ. Field Mus. Nat. Hist., Bot. Ser. **4,** 219, 1929) when he described *T. euryphyllum* from near Almirante (Prov Bocas del Toro). Since then, only two additional Panamanian collections of *Tetrorchidium* have been made; these represent a species different from *T. euryphyllum* in having smaller more prominently reticulate leaves. Perusal of the treatment of Colombian *Tetrorchidium* by Cuatrecasas shows that these recent Panamanian collections approach most closely *T. robledoanum* Cuatr. and *T. gorgonae* Croizat (Jour. Arnold Arb. **24:** 170, 1943). In fact, the foliar glands in one Panamanian collection (Canal Zone, W of Gatun Locks, *Johnston 1688,* MO) resemble those of *T. gorgonae* in being distinctly stalked and well below the apex of the petiole, whereas in the other collection (Panama, Cerro Jefe, *Duke 9415,* MO) the foliar glands are at the top of the petiole as in *T. robledoanum.*

In assessing the affinity of the Panamanian collections, it appears that they agree more closely with *T. robledoanum* in having smaller nearly entire leaves. The inconstancy of the foliar gland character in the Panama specimens, and the rather close resemblance of all the plants involved, suggests that the best course of action is to place all these taxa under the earliest name, *T. gorgonae,* with the mainland plants being assigned to a separate subspecies.—*Grady Webster, University of California, Davis.*

BERNARDIA AND CLEIDION (EUPHORBIACEAE) IN PANAMA

Bernardia **denticulata** (Standley) Webster, comb. nov.

Cleidion denticulatum Standley, Publ. Field Mus. Nat Hist., Bot. Ser. **4:** 218, 1929.

Beginning with Hemsley's description of *Cleidion nicaraguense* in 1873, a total of five species occurring in Panama have been referred to either *Bernardia* or *Cleidion*. Most of these are known only from one or few collections which are incomplete in several instances, so that the true generic affinities have remained obscure up to the present time. In the preceding note, Hemsley's species was disposed of by transferring it to *Acidoton;* it now remains to consider the others.

Croizat (Jour. Arnold Arb. **24:** 166, 1942) noted a strong resemblance to *Bernardia* in the pubescence and columella of *Cleidion denticulatum* Standl.; however, he apparently felt that the seeds were more like *Cleidion*. Actually, the large seeds of the type collection (*Cooper 606*, Chiriquí Trail, Bocas del Toro) are in size and shape not unlike those of, e.g., *Bernardia obovata* I. M. Johnston (as observed in *Johnston 3426*, DAV), although seeds of the Panama plant differ in being distinctly mottled.

While the generic position of the plant from Bocas del Toro cannot be fixed with absolute certainty in the absence of male flowers, I believe that the leaves, fruits, and seeds are all compatible with *Bernardia,* and that the dilated columella in particular mitigates against retaining the species in *Cleidion*.

The other species of *Bernardia* from Panama, *B. macrophylla* Standley, differs from *B. denticulata* in its less elongated and more finely toothed leaves. When (as observed in *Johnston 3426*, DAV), although seeds of the Panama plant differ ences.

Finally, although two of the three Panamanian species described in *Cleidion* have to be removed, *Cleidion woodsonianum* Croizat (Jour. Arnold Arb. **24:** 167, 1943) does appear to be a true *Cleidion*. Croizat himself later (Trop. Woods **88:** 31, 1946) transferred the species to *Adenophaedra*, but this action seems to be unwarranted. Examination of one of the isotypes (*Woodson et al. 1587*, Salamanca, Canal Zone; NY) yielded a single small ♂ inflorescence with a few buds; these prove to have numerous stamens (well over 50) as in *Cleidion*, in contrast to the two or three characteristic of *Adenophaedra*.

In summary, these various taxonomic changes leave the roster of Panama taxa at two species of *Bernardia* and one species of *Cleidion*. Additional material of all three species is needed before their affinities to their congeners can be appraised.

—*Grady Webster, University of California, Davis.*

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ERRATA

Page 33, line 41. For *A. filiformis* read *A. conferta.*

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FLORA OF PANAMA

BY

ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY

AND COLLABORATORS

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 85. GERANIACEAE[1]

BY BRUCE MACBRYDE

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St. Louis, Missouri

Herbs, perennial to annual, sometimes suffrutescent or shrubby, rarely arborescent; usually pubescent, the hairs simple and often also glandular. *Leaves* alternate or opposite, sometimes basal, simple or compound, usually stipulate; blades pinnately, palmately, or radiately cleft or parted, rarely entire, lobes variously toothed or incised. *Inflorescences* axillary to terminal, cymose or subumbellate, or the peduncle 1-few-flowered, bracteate. *Flowers* of small to medium size, ☿, actinomorphic to somewhat zygomorphic; sepals persistent, 5 (rarely 4 or 8), distinct to partially connate, imbricate or rarely valvate, often awned, the dorsal one sometimes with a nectiferous spur adnate to the pedicel; petals often deciduous, 5 (rarely 0, 2, 4 or 8), distinct, imbricate or rarely contorted, usually alternating with nectiferous disk glands; stamens (1), 2 or (3) times the number of sepals, usually obdiplosteminous, some frequently antherless or scalelike staminodia, the filaments often ± basally connate, rarely polyadelphous in threes, the anthers usually versatile, bithecate, dehiscing longitudinally; pollen grains various, with usually 0, 3 or >12 apertures; pistil solitary and deeply lobed, the ovary superior, the carpels and locules 3-5 (rarely 2 or 8), the placentation usually axile, the ovules 1-2 or ∞ per locule, pendulous, anatropous, the styles and stigmas isomerous with the carpels, the styles usually adnate to an elongated ovarian

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column, the stigmas free, usually ligulate. *Fruit* a capsule or schizocarp, usually dehiscing septicidally and elastically, often with mericarps attached to styles revolute from the base but terminally adherent to the column, the mericarps sometimes dehiscent; seeds 1 (2 or ∞), usually with little or no endosperm, curved embryo, and plicate to convolute incumbent cotyledons.

The *Geraniaceae* are treated conservatively to include the *Biebersteiniaceae, Dirachmaceae, Ledocarpaceae*, and *Vivianiaceae;* 11 genera and ca 800 species widely distributed in temperate and subtropical habitats, especially proliferating in South Africa, often somewhat xerophytic. Grown economically for their showy flowers, aromatic leaves, and as pasturage. While only one genus is native, some gardens in Panama probably display *Pelargonium* cultivars.

1. GERANIUM

Geranium L., Sp. Pl. 676, 1753.

Herbs, often with a woody root and rhizome terminating in a simple or diffusely branched caudex; stems repent to erect, dichotomously much branched to ± determinate and short, frequently with swollen joints. *Leaves* petiolate, the petiole sometimes articulate with the stipules or blade, basal and cauline leaves ± similar. *Flowers* regular, hypogynous; sepals 5, imbricate, not spurred; petals 5, white to pink, violet, or red, deciduous, sometimes clawed, reticulate-veined throughout or only apically, often basally pubescent, alternating with glands; stamens 10 (rarely 5), of two lengths, alternating, usually all antheriferous; pollen grains (2-)3-colp(or)ate; ovary 5-carpellate, the axile ovules 2 per locule, glandular epidermis of stigmas on inner tips. *Schizocarp* elastically septicidal, the revolute styles not twisting, the turgid mericarps dehiscent; seeds one per mericarp, plump and pitted, reticulate or smooth.

About 300 species growing in arctic, temperate, tropical mountainous, and antarctic regions, in wet to dry habitats. Wild animals forage some species of cranesbill, while the roots of others have been used medicinally as an astringent. Moore (Contr. Gray Herb. **146:** 1-108, 1943) recognized 43 (now 46) species from Mexico and Central America with two in Panama. Both of the Panamanian species have been frequently mistaken as *G. mexicanum* H.B.K. of Mexico.

a. From intermediate altitudes (1370-2000 m); stems erect to procumbent; blades dissected ½-¾ to the base, teeth short; flowers small, pedicels 5-15 mm long, petals 6-7 mm long by 2-4 mm wide, mature stigmas 1.5-2 mm long ....1. *G. guatemalense*

aa. From higher altitudes (ca 2500-3475 m); stems procumbent to repent; blades dissected nearly to the base, teeth moderately long; flowers large, pedicels 10-35 mm long, petals 10-14 mm long by 4-6 mm wide, mature stigmas 3 mm long ....2. *G. repens*

1. **Geranium guatemalense** Knuth in Engler, Pflanzenreich **53** (IV, 129): 200, 1912; emend. Moore, Contr. Gray Herb. **146:** 88, 1943.

Perennial *herbs;* roots fibrous to woody; stems to 2 m long and 4 mm thick, usually much branched, erect when young to ascending or prccumbent with ascending branches, sometimes scandent, sparsely to densely hirsute-pilose and some-

times glandular, lower and upper portions ± similar. *Leaves* basal and cauline, the basal not long-persistent, petioles to 24 cm long, pubescent as the stems, stipules subulate, attenuate, sometimes cleft, to 1.2 cm long, puberulous and ciliate; blades darker above, broadly pentagonal to rarely almost deltoid in outline, 1-6 cm wide, divided ½ to often ¾ to the base into 5 (or sometimes 3) rhombic lobes, the sublateral sinuses often less deep than the subapical, lobes once- or twice-cleft, toothed above the middle with short, mucronate to acute, lanceolate segments, lateral lobes often with a basal lobelet, hirsute to strigose above, spreading-hirsute to long-pilose on the veins below. *Inflorescences* with 2-flowered peduncles, single and axillary or tending to cymose clusters at the tips of older branches, the peduncles 1-5 cm long, pilose and copiously long-glandular. *Flowers* white to lavender, with darker veins, the pedicels 5-15 mm long, pubescent as the peduncles, erect in fruit; sepals 4-5 mm long with awn to 1 mm, enlarged in fruit, ovate-lanceolate and 3-veined, the veins and margins glandular-pilose; petals obovate, 6-7 mm long, 2-4 mm wide, the base short-pilose with lateral tufts, the apex usually shallowly notched, veins slightly reticulate (stronger apically); stamens shorter than the sepals, the outer whorl shortest, the filaments basally flattened, hirsute. Mature *fruits* 18-23 mm long, mericarps 3 mm long, hirsute and glandular, column hispidulous and glandular, stigmas 1.5-2 mm long; seeds 2-2.5 mm long, the testa dark brown to black and reticulate.

Collected from intermediate altitudes throughout Guatemala, and in El Salvador, Costa Rica, and western Panama, where presently found from 1370-2000 m in rain forest to clearings. The species is closely related to *G. seemannii* Peyr. of Mexico.

CHIRIQUÍ: vic of "New Switzerland", central valley of Río Chiriquí Viejo, alt 1800-2000 m, *Allen 1380* (MO, US); way to "Lérida" (Boquete), alt 4500 ft, *Bro. Maurice 899* (US); Bajo Chorro, Boquete Dist, alt 6000 ft, *Davidson 303* (MO, US); valley of the Río Chiriquí Viejo, N Volcán City, alt 5200-5600 ft, *Duke 9009* (MO); Río Chiriquí Viejo valley, nr El Volcán, *White 183* (MO, US); vic of Casita Alta, Volcán de Chiriquí, alt ca 1500-2000 m, *Woodson et al. 893* (MO).

2. **Geranium repens** Moore, Contr. Gray Herb. **146:** 78, 1943.—Fig. 1.

G. pulchrum Morton, Phytologia **1:** 147, 1935, non N. E. Brown (Kew Bull. **1895:** 143, 1895).

Perennial *herbs;* roots woody-fibrous, horizontal rhizome short to long, slender; stems to at least 0.8 m long, to 2.5 mm thick, much branched, procumbent with ascending branches, often rooting at the nodes, glabrate to densely strigillose or short-pilose and often glandular. *Leaves* basal and cauline, the basal not long-persistent, petioles to 25 cm long, strigose to pilose, stipules subulate, attenuate, sometimes cleft, to 1 cm long, strigillose and ciliate; blades darker above, orbicular to broadly pentagonal or almost deltoid in outline, 1-5 cm wide, divided nearly to the base into 5 (sometimes 3 or 7) usually rhombic lobes, the sublateral sinuses sometimes less deep than the subapical, lobes once- or twice-cleft, toothed above the middle with moderately long, mucronate to acute, lanceolate segments, closely strigillose to pilose above, strigose to pilose on the veins below. *Inflorescences* with

Fig. 1. *Geranium repens* Moore: A, habit (× 5/9); B, flower (× 2¾). A after *Woodson & Schery 378* (MO); B also after *Davidson 1007* (US).

2-flowered peduncles, single and axillary, the peduncles 1-5(-10) cm long, open- or retrorse-pilose to strigose and often glandular. *Flowers* white to lavender, with darker veins, the pedicels 10-35 mm long, short-pilose and long-glandular, divaricate in fruit; sepals 5-6 mm long with blunt-tipped awn to 1 mm, enlarged in fruit, ovate and 3-veined, often tinged violet, antrorse-strigillose, the veins and margins also long-glandular; petals narrow-obovate, 10-14 mm long, 4-6 mm wide, the base very short-pilose, the apex shallowly to deeply notched, veins very slightly to moderately reticulate throughout; stamens shorter than the sepals, the outer whorl shortest, the filaments basally flattened, hirsute. Mature *fruits* 18-21 mm

long, mericarps 2.5 mm long, hirsute, column hispidulous or short-pilose and glandular, stigmas 3 mm long; seeds 2-3 mm long, dark brown, reticulate.

Collected from higher altitudes in southern Mexico, Guatemala, Costa Rica, and western Panama, where presently known from ca 2500-3475 m on El Volcán de Chiriquí.

CHIRIQUÍ: Potrero Muleto, Volcán de Chiriquí, Boquete Dist, alt 10,400 ft, *Davidson 1007* (MO, US); above Potrero Camp, Chiriquí Volcano, alt 2900 m, *Killip 3592* (US); around El Potrero Camp, Chiriquí Volcano, alt 2800-3000 m, *Pittier 3096* (US); Loma Larga to summit, Volcán de Chiriquí, alt ca 2500-3380 m, *Woodson et al. 1049* (MO); Potrero Muleto to summit, Volcán de Chiriquí, alt 3500-4000 m, *Woodson & Schery 378* (MO).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 94. TRIGONIACEAE[1]

BY DANIEL F. AUSTIN

Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Trees or scandent shrubs; branchlets terete or angulate. *Leaves* simple, opposite or alternate, entire; blades pinnately veined; stipules usually present, deciduous, interpetiolar, sometimes connate. *Inflorescences* thyrsiform, paniculate or racemose. *Flowers* small, ☿, irregular, bibracteolate; sepals 5, free or connate at base, unequal, imbricate in bud; petals 3 or 5, white or pink, contorted in bud, hypogynous or subperigynous, alternate with sepals, unequal, posterior often largest and gibbous or spurred at base; stamens 5-12 with 2-6 of the fertile ones united, the tube being cleft opposite the spurred petal, the anthers 2 or 4-celled, opening by longitudinal introrse slits; disc glands present opposite the spurred petal; ovary superior, 3-celled, wooly, the ovules 2-∞ in each cell, biseriate, axile, anatropous, the style terminal, simple, the stigma capitate or obliquely truncate. *Fruit* capsular, 3-celled, septicidally 3-valvate, the valves separating from the central column and themselves often separating into epicarp and endocarp; seeds 2-∞ in each cell, testa thin, compressed, covered with long wool, endosperm present, the embryo straight, transverse to the length of the seed, cotyledons plane, thin, radicle short.

A tropical family of four genera: *Trigonia, Lightia, Trigoniastrum,* and *Humbertodendron.* Only *Trigonia* is found in Panama.

1. TRIGONIA

Trigonia Aublet, Hist. Pl. Gui. Fr. 387, 1775.

Hoeffnagelia Neck., Elem. Bot. **3:** 68, 1790.
Nuttallia Spreng., Neue. Entdeck. **2:** 158, 1821.
Mainea Vell., Fl. Flum. 275, 1825.

Shrubs, scandent or reclinate. *Leaves* short-petiolate; stipules interpetiolar, deciduous, simple or bifid at apex, free. *Inflorescences* thyrsiform, with untimate divisions consisting of cymes. *Flowers* small, irregular, mostly white; sepals connate at base, unequal, 2 inner larger; petals distinct, very unequal, the posterior

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

one largest, spurred or saccate, pilose in throat of spur, blade reflexed, the 2 anterior ascending, inequilateral, narrow, barbate above the base, the 2 others smaller, approximate and keel-like; stamens 10, but usually only 6 fertile, opposite anterior petals, the anthers oblong; disc glands 2-4 or a crenate crest opposite the posterior petal; ovary ovoid or subglobose, attenuate to the style, hirsute. *Capsule* 3-angulate, often hairy outside and often also within, with several compressed-globose seeds in each cell.

A tropical genus of about 25 species.

1. **Trigonia floribunda** Oersted, Dansk Naturh. Foren., Copenh. Vide. Meddel. 38, 1856.—Fig. 1.

T. rigida Oersted, loc. cit.
T. thyrsifera J. D. Sm., Bot. Gaz. **23:** 3, 1897.
T. panamensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 346, 1940.

Shrubs, large, scandent or subscandent; branchlets tetragonous or terete, densely arachnoid-tomentose at first but becoming glabrate. *Leaves* with blades elliptic-oblong, oval-oblong, lance-oblong, or obovate-oblong, 5-15 cm long, 1.5-8 cm wide, acute to rounded apex, acute or obtuse at base, chartaeous, becoming green and glabrate above except along veins, covered below with dense white tomentum, but in age with mostly only ascending adpressed hairs on veins and lamina sparcely scabrous, the venation prominent beneath with lateral nerves 8-9 pairs, arcuate-ascending, anastomosing near margins; petioles stout, subcanaliculate, 0.5-2 cm long, tomentose or glabrate. *Inflorescences* thyrsoid-paniculate, exceeding leaves, the thyrses 10-25 cm long, the rachises tomentose or glabrate, the cymules ± dichotomous. *Flowers* white, ☿, the pedicels to 2 mm long; sepals lance-oblong, acute, 3-4 mm long, grayish-green pubescent without, glabrous within; petals white, 3-4 mm long, the spur ± globose, 2 mm long, extruded between calyx lobes in bud, lateral petals linear-spathulate, apex rotund; stamens 6, glabrous, shorter than petals; disc glands 2-4; ovary ovoid, villous, the style ca 1 mm long, the stigma obliquely truncate. *Capsules* 20-22 mm long, 14-16 mm wide, dark, rugose, glabrous, with outside coriaceous and inside cartilagenous flavescent smooth, apex bifid; seeds 6-9, oval, in each locule, covered with long, yellowish, silky hair.

Found from about 100-1000 m, from Chiapas, Mexico to Colombia; a very variable, little-collected, little-understood species.

CANAL ZONE: Fairchild Point on Barro Colorado I, *Aviles 961* (F); Barro Colorado I, *Frost 175* (F). DARIEN: vic of Yavisa, along Río Chucunaque, *Stern et al. 163* (MO); vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa nr Quebrada Felix, *Stern el al. 953* (MO); along trail from Paya to Pucre, *Stern et al. 224* (MO). Flw June—July.

Fig. 1. *Trigonia floribunda* Oersted: A, habit (ca × 5/9); B, back of flower showing spurred banner-like petals in lower center, wing-like petals on sides, and keel-like petals at top (ca × 11); C, front side of flower (ca × 13); D, gynoecium (ca × 13); E, androecium (ca × 13). After *Stern et al. 224* (MO).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 97. EUPHORBIACEAE[1]

BY GRADY L. WEBSTER[2] AND DEREK BURCH[3]
University of California, Davis, California and
Missouri Botanical Garden, St. Louis

Trees, shrubs, herbs, or vines; stems sometimes succulent, sometimes with milky or colored sap. *Leaves* alternate or, less commonly, opposite (rarely whorled), petiolate; stipules free or connate, often caducous, obsolete or absent; blades pinnately or palmately veined, compound or simple and lobed or not. *Inflorescences* cymose, racemose, or spicate, sometimes aggregated in pseudanthia. *Flowers* unisexual, mostly actinomorphic; calyx in most taxa of 3-6 valvate or quincuncially imbricate lobes or segments, rarely absent; corolla of 3-6 petals, or often reduced or absent; glandular disc of receptacular or staminodal origin often present; stamens (1-)3-20(-400 or more), the filaments free or united, the anthers mostly 2-locular and dehiscing longitudinally; pollen grains most often 3-colporate but sometimes inaperturate or polytreme; gynoecium of (1-)3 or 4(-20) united carpels, the ovary superior, with axile placentation, the ovules 1 or 2 per locule, anatropous or hemitropous, epitropous, inserted beneath an obturator, crassinucellate, often with a nucellar beak. *Fruits* typically capsular, of 3 elastically dehiscing cocci separating from a persistent columella but sometimes drupaceous (rarely baccate or samaroid); seeds 1 or 2 per locule, or (by abortion) solitary in the fruits, the seed coats crustaceous to bony, the endosperm usually copious (rarely absent), the embryo extending most of the length of the seed, the cotyledons usually broader than the radicle, plane or rarely folded.

A highly diversified family of at least 7,000 species in more than 300 genera. Despite the relative floristic poverty of Panama, it has an impressive array of 36 genera with native species and a few additional genera, such as *Pausandra*, may still be discovered during the course of further exploration. A considerable variety of exotic euphorbiaceous genera are presently cultivated in Panama, especially in the Canal Zone, and a few of these may eventually escape to a certain extent as

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[2] Responsible for Genera 1-25.

[3] Responsible for Genera 26-36.

ANN. MISSOURI BOT. GARD. **54**: 211-350, 1967 [1968].

components of the native vegetation. Exotic genera in the *Phyllanthoideae* include *Antidesma* and *Breynia*, while the *Euphorbioideae* are represented by *Aleurites*, *Codiaeum*, and *Hevea*.

Useful references:

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Key to the Genera

a. Ovules paired in each cell of the ovary; sap never milky; leaves entire, unlobed, not glandular. [Subfam. *Phyllanthoideae*]
  b. Petals present; stipules intra-petiolar; fruits massive, 2 cm long .....1. *Amanoa*
  bb. Petals absent; stipules not intra-petiolar; fruits smaller, rarely exceeding 1 cm long.
    c. Indumentum of simple or branched hairs; fruits of 3 or more carpels, not indehiscent and 1-seeded; ♂ flower without pistillode.
      d. Fruit of 4 or 5 (rarely 3) carpels, irregularly dehiscent; seeds with bluish fleshy outer coat and bony inner coat; ♂ flower with annular disc and 4 free stamens; dioecious shrub or tree .....2. *Margaritaria*
      dd. Fruit of 3 (rarely 2 or 4) carpels, dehiscent in most species; seeds neither fleshy nor bony; ♂ flower with stamens 3 or else disc absent (in local taxa); monoecious or dioecious, habit various ....3. *Phyllanthus*
    cc. Indumentum lepidote; fruit of 2 carpels, drupaceous, 1-seeded; ♂ flower with pistillode .....4. *Hyeronima*
aa. Ovules solitary in each cell of the ovary; sap often colored or milky; leaves often lobed and/or with petiolar glands or marginal teeth. [Subfam. *Euphorbioideae*].
  e. Flowers not aggregated into pseudanthia.
    f. Stamens fasciculate-ramified, anthers ∞; leaves peltate, palmately lobed; inflorescences terminal, paniculate; ♀ flowers distal .....23. *Ricinus*
    ff. Stamens not highly branched, anthers equal in number to stamens; leaves not peltate and palmately lobed; inflorescences terminal or lateral, not paniculate, if ☿, with ♀ flowers proximal (lower).
      g. Inflorescences of small clusters of stalked globose involucres each enclosing 3-10 sessile flowers (involucres almost lacking in one species but form of inflorescences otherwise the same) .....26. *Pera*
      gg. Inflorescences not of pedunculate heads of sessile flowers.
        h. Petals present at least in ♂ flowers, often conspicuous in both ♂ and ♀.

i. Anthers ± erect in bud, not distinctly inflexed; indumentum not lepidote or of branched hairs (except trichomes malpighiaceous in *Argythamnia*).
j. Stamens not over 10.
k. Inflorescence dichasial; seeds carunculate; pollen grains verrucose; leaves palmately veined or lobed .....5. *Jatropha*
kk. Inflorescence racemiform; seeds ecarunculate; pollen grains not verrucose, 3-6-colporate; leaves pinnately veined.
l. Leaves finely serrate, lateral veins distinctly parallel; trichomes simple or glandular (not malpighiaceous); pistillode present in ♂ flower .....10. *Caperonia*
ll. Leaves entire, lateral veins not distinctly parallel; trichomes malpighiaceous (at least in part); pistillode absent in ♂ flower .....11. *Argythamnia*
jj. Stamens ∞ (50 or more) .....6. *Garcia*
ii. Anthers distinctly inflexed in bud; indumentum (at least in part) of lepidote or branched hairs .....9. *Croton*
hh. Petals reduced or absent in both ♂ and ♀ flowers.
m. Calyx distinctly petaloid; inflorescences dichasial.
n. Stinging hairs absent; ♂ flowers usually yellowish or greenish to purplish, stamens free, the disc intrastaminal .....7. *Manihot*
nn. Stinging hairs present (sometimes very sparse); ♂ flowers whitish, stamens connate, disc extrastaminal .....8. *Cnidoscolus*
mm. Calyx not petaloid; inflorescences not obviously dichasial.
o. Styles connate, columnar, 2.5-5 cm long terminating in a fleshy disc 2-3 cm wide; ♂ flowers aggregated into a pedunculate fleshy cone; carpels more than 5 .....32. *Hura*
oo. Styles usually much shorter than 2.5 cm, if long-columnar then not ending in a broad disc; ♂ flowers not aggregated into a fleshy cone; carpels usually less than 5, if more the fruit pome-like.
p. Floral bracts not with conspicuous paired basal glands; ♂ calyx-lobes valvate (imbricate in *Omphalea*).
q. Not twining with stinging hairs; ♂ flowers with 3 or more stamens (often 2 in *Omphalea*).
r. Carpels 2; styles elongated, free, ± entire and unlobed; stamens usually 8 .....15. *Alchornea*
rr. Carpels 3 or 4, styles variously modified, stamens few or many, not consistently 8.
s. Shrubs or trees, not lianas; styles free or at least not united for most of their length into a column.
t. Anthers not vermiform; ♀ bracts not strikingly larger or different from the ♂; inflorescences racemose or thysoid, not definitely spicate.
u. Stamens over 10.
v. Stamens over 50, ♀ pedicel slender, 10-15 mm long styles bifid .....14. *Cleidion*
vv. Stamens not over 35.
w. Stamens 24-35, anthers with a minute apical tuft of stinging hairs; styles connate into a column, the ends undivided, papillose .....19. *Acidoton*
ww. Stamens less than 20, anthers without an apical tuft of stinging hairs, styles free or nearly so.
x. Styles deeply laciniate; ♀ pedicels becoming 20-70 mm long; leaves without basal foliar glands .....12. *Adelia*
xx. Styles 1 or 2 times bifid; ♀ flowers sessile or subsessile; leaves with conspicuous foliar glands near the base .....13. *Bernardia*

uu. Stamens less than 10.
y. Disc absent in ♂ flower; stamens 3, anthers peltate, 4-locellate .....17. *Tetrorchidium*
yy. Disc of ♂ flower massive, central stamens 4-8, not peltate.
z. Pistillode present in ♂ flower; leaves triplinerved; fruits small, seeds compressed and with fleshy coat, less than 3 mm long .....16. *Alchorneopsis*
zz. Pistillode absent in ♂ flower; leaves pinnately veined; fruits massive, seeds spheroidal, 15 mm long or more, seed coat not fleshy .....18. *Caryodendron*
tt. Anthers vermiform; ♀ bracts much larger than ♂ (or if not, ovary dense-verrucose); flowers spicate .....24. *Acalypha*
ss. Lianas; styles connate for most of their length into a column.
A. Stamens 19-24; ♂ calyx-lobes valvate; carpels 4, carinate; seeds lenticular, 15-17 mm broad; leaves acuminate .....21. *Plukenetia*
AA. Stamens 2(-3); ♂ calyx-lobes imbricate; carpels 3, sericeous; seeds compressed, 39-40 mm broad; leaves obtuse .....22. *Omphalea*
qq. Twining vine armed with stinging hairs; ♂ flowers with 2 stamens ....20. *Tragia*
pp. Floral bracts with conspicuous basal glands; ♂ calyx-lobes imbricate or open.
B. Seed carunculate, dry; fruit capsular; petiole eglandular but sometimes with cupular glands at base of leaf blade.
C. Inflorescence spicate.
D. Columella with a persistent hardened gynobase; ♂ calyx lobes and stamens 2 .....29. *Stillingia*
DD. Columella without hardened gynobase after dehiscence of fruit; ♂ calyx-lobes and stamens usually 3 .....27. *Sebastiania*
CC. Inflorescence racemiform or paniculate .....28. *Mabea*
BB. Seed ecarunculate, either seed coat or capsule wall fleshy; petiole usually biglandular, the stipitate glands a little below the junction with the blade.
E. Fruit thin walled, capsular; seed coat fleshy; ovary 3 locular .....30. *Sapium*
EE. Fruit fleshy, indehiscent; seed coat dry; ovary 6-10 locular ....31. *Hippomane*
ee. Flowers aggregated into pseudanthia (see also 26. Pera).
F. Pseudanthium bilabiate, the flowers subtended by 2 large divergent palmately veined bracts; ♀ flowers 3 at lower node, ♂ 6-12; styles connate to the stigmas; fruiting calyx covered with irritating hairs; vines ....25. *Dalechampia*
FF. Pseudanthium radially symmetrical, or if bilaterally symmetrical then not subtended by divergent bracts; ♀ flower solitary, terminal, ♂ in 5 groups around base of ♀; styles free or connate; calyx obsolete; herbs, shrubs, or trees, never twining.
G. Cyathium spurred, strongly zygomorphic; glands hidden within spur .....36. *Pedilanthus*
GG. Cyathium not spurred, overall appearance ± actinomorphic; glands on rim of cyathium.
H. Glands of cyathia solitary (rarely up to 5 on first few formed), exappendiculate .....34. *Poinsettia*
HH. Glands of cyathia usually 4 or 5, exappendiculate or with petaloid appendages.
I. Leaves all opposite, base inequilateral, veins chlorenchyma-sheathed, stipulate; main axis aborting within 2 nodes of cotyledons .....35. *Chamaesyce*
II. Leaves alternate, opposite or whorled, if opposite base ± equilateral, veins not chlorenchyma-sheathed, stipules often obsolete; main axis persisting or aborting only after an obvious stem has been produced .....33. *Euphorbia*

1. AMANOA

Amanoa Aublet, Hist. Pl. Gui. Fr. 256, *t. 101*, 1775.

Trees or shrubs, glabrous; monoecious. *Leaves* alternate, coriaceous, entire; short-petiolate; stipules persistent, oblique-decurrent, projecting between adaxial surface of petiole and stem ("intrapetiolar"). *Inflorescences* subsessile or shortly pedicellate, the densely bracteate clusters racemose or occasionally paniculate; sepals 5, firm, larger than the sometimes scale-like petals; disc not very conspicuous. *Staminate flowers* with stamens 5, the filaments free, shorter than the introrsely dehiscing anthers; pollen grains oblate, 3-5-colporate, echinate; pistillode conspicuous. *Pistillate flowers* with 3 carpels, the ovules 2 in each locule, anatropous, the styles connate, the stigmas thick, bifid, reflexed. *Fruits* capsular, massive, the endocarp often very thick, tardily dehiscent, the columella massive, tapering from the base; seeds usually 3 per capsule, ovoid or ellipsoid, smooth, not carunculate, thin-walled, the endosperm scanty or absent, the massive angled cotyledons filling most of the seed, the radicle short.

A small but somewhat heterogeneous genus of about 10 American and African species. The three African species are distinguished by larger floral bracts but on the whole appear to be correctly placed in the same genus as the neotropical taxa.

1. **Amanoa guyanensis** Aublet, Hist. Pl. Gui. Fr. 256, *t. 101*, 1775.—Fig. 1.

Tree, glabrous; twigs smooth, terete or somewhat angled. *Leaves* coriaceous; petiole 5-8 mm long, adaxially deeply furrowed; stipules inconspicuous, reddish, ca 1 mm high; blades elliptic to elliptic-oblong, rather abruptly cuspidate or acuminate, 8-13 cm long, 4.5-7 cm broad, rounded or obtuse to subcordate at the base, with 8-13 major and several minor veins on each side. *Inflorescences* on stiff lateral branchlets or branch-tips, subtended by reduced leaves or by scale-like bracts. *Staminate flowers* with pedicel shorter than the calyx; calyx-lobes 5, thick, ovate, ca 7-9 mm long; petals dark, unguiculate, ca 0.7-1 mm long, 1.1-1.4 mm broad; disc cupuliform, shallow, margin thin, undulate; anthers ca 5 mm long; pistillodes massive, apically 3-lobed, ca 5 mm high, 2.5 mm in diam. *Pistillate flowers* with stout pedicel, becoming 1.5 cm long; calyx-lobes ovate-oblong, ca as long as in ♂; petals suborbicular, shortly unguiculate, finely denticulate, 1.5-1.7 mm long, 2-2.3 mm broad; ovary abruptly or gradually passing into the thick stylar column, the stigmas dilated, reflexed, ± crenulate at the ends. *Capsule* 2 cm long (in Panamanian specimen), thick; seeds ovoid, 1-1.5 cm long.

Rainforests, northern South America.

CANAL ZONE: nr mouth of Río Chagres, flooded land, *Johnston 1698* (GH, MO).

It seems rather remarkable that this species has been collected only once, since the collector noted that it was frequent in an area which has often been botanized. The identification of the Johnston collection as *Amanoa guyanensis* is made with some hesitation, since the specimen does not include flowers. The Panamanian plant appears to be quite similar to that from British Honduras determined by

Fig. 1. *Amanoa guianensis* Aublet: A, habit (ca ×½); B, male flower (ca ×7); C, female flower (ca ×5); D, ovary (ca ×7). After *La Cruz 2514* (MO), British Guiana.

Standley (Trop. Woods **32:** 15, 1932) as *A. grandiflora* Muell.-Arg. and made the type of a new species *A. potamophila* by Croizat (Amer. Midl. Nat. **29:** 476, 1943). Until the neotropical populations of *Amanoa* can be carefully studied and the distinction between *A. guyanensis* and *A. grandiflora* worked out more satisfactorily, any identification of the Panamanian population must be provisional.

2. MARGARITARIA

Margaritaria L. f., Suppl. Pl. Syst. Veg. 66, 1781.

Shrubs or trees; dioecious; foliage deciduous, new leaves appearing with flowers (or persistent in certain species), ramification distichous, branches all persistent with ± conspicuous lenticels. *Leaves* alternate, entire, chartaceous; short-petiolate; stipules entire, subpersistent. *Inflorescences* of clustered flowers on short floriferous branches or at proximal axils of leafy branches, rarely flowers solitary; gamosepalous, the calyx-lobes usually 4; apetalous; disc annular and entire in both sexes. *Staminate flowers* with long pedicels; stamens usually 4, free, the anthers extrorse in the bud, dehiscing longitudinally; pollen grains 3-colporate. *Pistillate flowers* with stout pedicels; ovary with 2-5 carpels, the styles free or united into a column, bifid to bipartite, ± dilated. *Capsules* irregularly dehiscent, the green reticulate exocarp usually breaking away from the pale membranous endocarp of each coccus, the cocci very fragile, fragmenting irregularly; seeds normally paired in each coccus, the outer seed-coat dark blue, thick and fleshy, the inner seed-coat thick and woody, achene-like, smooth or rugose, invaginated at the chalazal end, the endosperm copious, whitish, the embryo straight or nearly so, the cotyledons thin and flat, much longer than the radicle.

A very homogeneous genus of about 10 species, represented in most tropical regions except Australia and the Pacific Islands. Mueller (in DC., Prodr. **15**(2): 414-418, 1866), on the basis of the tetramerous flowers, treated the group as three subsections of his sect. *Cicca* L., which also included the common *Phyllanthus acidus* (L.) Skeels. This unnatural arrangement has misled the majority of subsequent workers into treating *Margaritaria* as a section within *Phyllanthus*. Actually, however, it more closely resembles certain other genera of *Phyllantheae* such as *Flueggea* and *Securinega* than it does any species of *Phyllanthus*.

1. **Margaritaria nobilis** L. f., Suppl. Pl. Syst. Veg. 428, 1781.—Fig. 2.

Cicca antillana Juss., Tent. Euphorb. 108, *t. 4 fig. 13B*, 1824.
Phyllanthus antillanus (Juss.) Muell.-Arg., Linnaea **32:** 51, 1863.
P. nobilis (L. f.) Muell.-Arg. in DC., Prodr. **15**(2): 414, 1866.
P. nobilis var. *hypomalacus* Standley, Carn. Inst. Wash. Publ. **461:** 68, 1935.

Tree 5-10 m high; dioecious; branches subterete or angled, glabrous, usually with conspicuous lenticels. *Leaves* chartaceous; petioles ca 2-5 mm long; stipules elliptic to oblong, acuminate, 1.5-3 mm long; blades elliptic or oblong to ovate-lanceolate, ca 6-15 cm long, 2.5-5 cm broad, smooth above, glabrous or glaucous beneath and sometimes hairy along the veins, major veins mostly 7-12 on a side,

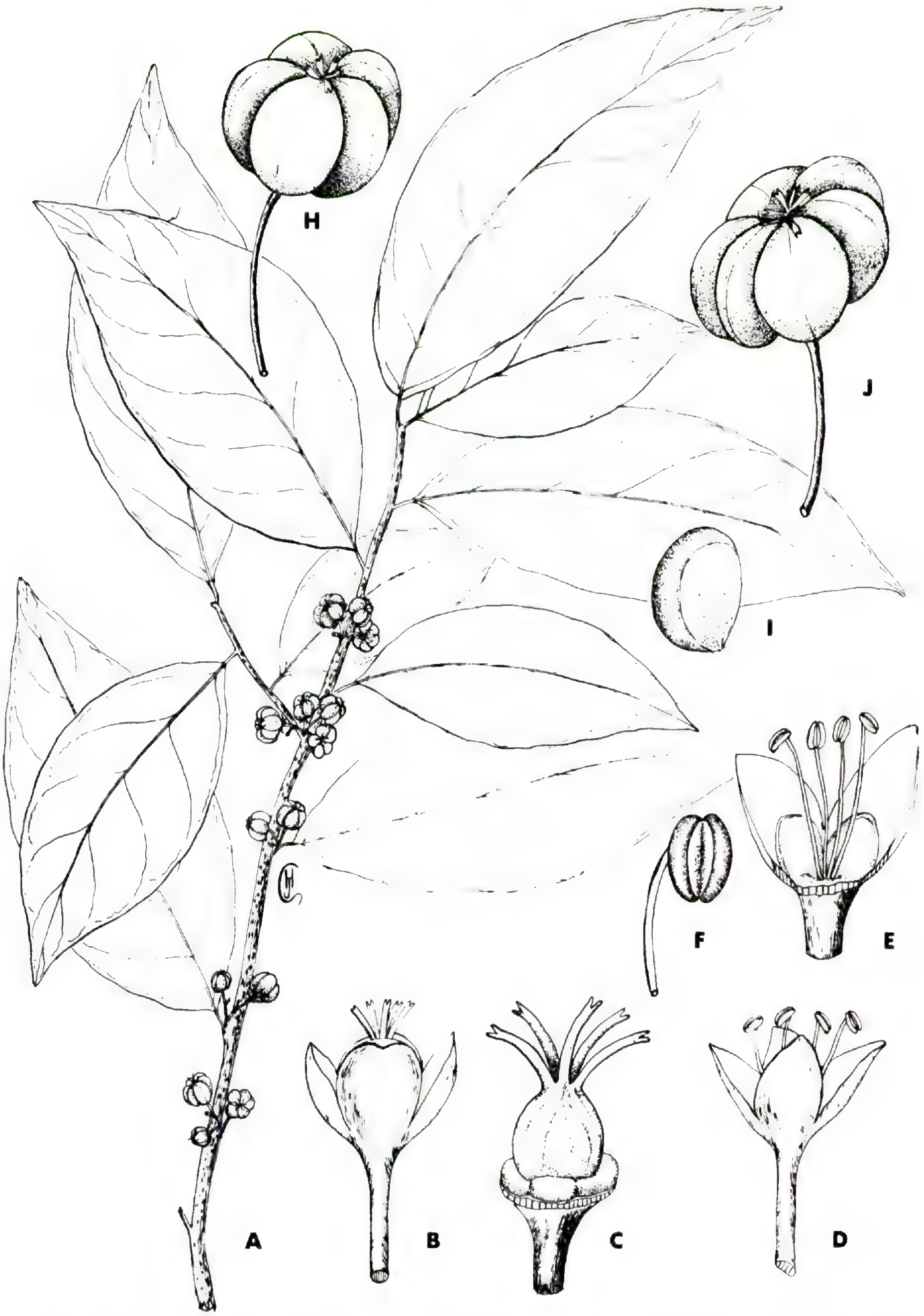

Fig. 2. *Margaritaria nobilis* L. f.: A, habit (×½); B, female flower (×5); C, ovary (×8); D, male flower (×5); E, stamens (×8); F, anther (×20); J. fruit with 6 locules (×3); H, fruit with 5 locules (×3); I, seed (×5). A after *Duke 5040* (MO); B-C after *Woodson et al. 1364* (F, GH, MO); D-F after *Broadway 4515* (MO), Tobago; H-I after *White 164* (MO).

raised beneath, the veinlets scarcely raised beneath but often conspicuous, cuneate to rounded at the base, ± acuminate at the tip. *Inflorescences* of 2-several flowers per cluster or the ♀ sometimes solitary. *Staminate flowers* with pedicels ca 2.5-5 mm long; calyx-lobes 4, somewhat unequal (outer pair usually narrowly membranous), ca 0.9-1.7 mm long; anthers ca 0.4 mm long. *Pistillate flowers* with pedicels rather stout, becoming 5-14 mm long in fruit; calyx-lobes 4, similar to the staminate; disc 0.8-1.5 mm broad; ovary usually of 4 or 5 (rarely 3) carpels, the styles ca 1.5 mm long. *Capsules* mostly 8-11 mm in diam; seeds ca 3.5-4 mm long.

Mexico and Cuba south to Peru and Brazil, in both wet and dry forests.

BOCAS DEL TORO: Almirante, *Cooper 381* (F), Changuinola, *Dunlap 19* (F, US). CANAL ZONE: Albrook, *Dwyer 7124* (MO); Barro Colorado I, *Shattuck 975* (MO, NY), *Standley 41045* (US); Cerro Gordo, *Standley 25988* (US); Chagres River, *Pittier 3468* (US); Fort Hamilton, *Maxon & Harvey 6531* (US); Fort Sherman, *Standley 30975* (US); Gamboa, *Pittier 6650* (US); Gatun, *Hayes 219* (NY); Miraflores, *G. White 164* (MO, NY), *P. White 131* (F, MO); Sosa Hill, *Duke 4708* (MO). CHIRIQUÍ: Cerro Galera Chorcha, vic of Gualaca, *Allen 5018* (F, MO). DARIEN: El Real, *Duke 5040* (MO), *Stern et al. 892* (MO); vic of El Real, Río Tuira, *Stern et al. 768* (DAV, MO); La Palma, *Pittier 6603* (US); Río Chucunaque, vic of Campamento Buena Vista, *Stern et al. 919* (DAV, MO), betw Río Membrillo and Río Subcuti, *Duke 8599* (MO), *8611* (MO); vic of Santa Fé, Río Sabana, *Duke 4154* (MO). PANAMA: Arraiján, *Woodson et al. 1364* (F, GH, MO); Bella Vista, *Maxon & Valentine 6950* (US); Punta Paitilla, *Standley 30813* (US); Río Mamonica, 4 mi beyond Chepo, *Duke 5577* (MO); Río Tocumen, *Standley 26725* (US); Sabana de Juan Corso, *Pittier 4518* (F, US); San José I, *Johnston 954* (GH, MO). SAN BLAS: headwaters of Río Malatupu, *Elias 1743* (MO, GH), *1750* (MO, GH, US).

This very widespread but not necessarily common plant exhibits a great deal of geographic variation. Mueller (in DC., Prodr. **15**(2): 414-415, 1866; in Mart., Fl. Bras. **11**(2): 70, 1874) recognized a considerable number of varieties which have not been listed in the synonymy of the species, as most of these are South American and have not yet been evaluated. The "variety" *hypomalacus* from Central America described by Standley is merely a sporadic pubescent form unworth of taxonomic recognition. The plant described from Colombia as *Phyllanthus heteromorphus* (Rusby, Descr. S. Amer. Pl. 42, 1920) is perhaps the most distinctive geographic race due to its striking pubescence, but it has not been encountered in Panama.

Very closely related to *M. nobilis* is an African species, *Margaritaria discoidea* (Baillon) Webster. Like *M. nobilis*, the African species is widespread and very polymorphic. It is very difficult to find a single character which will separate all specimens of both species, but *M. discoidea* usually differs in having carpels mostly 3 (rarely 4, apparently never 5), shorter fruiting pedicels (3.5-6 mm) and smaller seeds (mostly 2.6-3.3 mm long). In the West Indies (Cuba, Bahamas, and Hispaniola) occur three endemic species of *Margaritaria* which are probably closely related to *M. nobilis*. All of these, however, differ in having scabridulous branchlets, and *M. scandens* (Wright ex Griseb.) Webster, the species most easily confused with *M. nobilis*, has obtuse leaves whitened with waxy points beneath. Evidently the morphological differentiation of populations has occurred with extreme slowness in *Margaritaria*, so that populations isolated for long geological periods have not diverged greatly.

3. PHYLLANTHUS

Phyllanthus L., Sp. Pl. 981, 1753; Gen. Pl. ed. 5, 422, 1754.

Trees, shrubs or herbs of very diverse habit; monoecious or subdioecious, much less commonly dioecious; branching unspecialized (twigs then persistent, with spiral or distichous phyllotaxy) or (in many species) axes of two kinds: persistent, with spiral phyllotaxy and without flowers, and deciduous, with distichous phyllotaxy and often floriferous. *Leaves* usually alternate, entire, varying in size and texture; short-petiolate; stipules deciduous or persistent. *Inflorescences* usually axillary; flowers solitary or in reduced cymes, in some species cauliflorous or in pseudoterminal thyrses; gamosepalous, 4-6 lobed; apetalous; disc usually present. *Staminate flowers* with mostly 3-6(2-15) stamens, the filaments free or connate; disc usually cut into segments; pollen grains sometimes spheroidal and 3-colporate but often with other patterns, small, intectate; pistillode absent. *Pistillate flowers* pedicellate or subsessile; calyx-lobes usually 5 or 6, usually entire; disc entire or cut into segments, rarely absent; carpels usually 3, the ovules 2 per locule, hemitropous, the styles free or united, bifid or variously divided or dilated. *Fruits* usually capsular, ± explosively dehiscent, less commonly baccate or drupaceous, the crustaceous cocci separating from a persistent columella; seeds usually 2 per locule (rarely only 1 developing), the seed-coat dry and crustaceous, smooth or sculptured, the endosperm cartilaginous, the embryo straight or slightly curved.

A diversified genus of perhaps 700 species, the majority of these belonging to the Old World. The genus has been subdivided by many authors, but the broad concept of Mueller-Argoviensis has been retained by most recent workers. The species may be grouped into about 10 subgenera, of which six are represented in Panama by either wild or cultivated species. The local species fall into two basically different types: those in subg. *Isocladus* Webster, with distichous leaves and undifferentiated branching, and the other species with deciduous and often floriferous branchlets; the latter have been designated as having 'Phyllanthoid' branching (Webster, Jour. Arnold Arb. **37:** 102-114, 1956).

The so-called grosella or Otaheite gooseberry, *P. acidus* (L.) Skeels, is rather commonly cultivated in Panama and elsewhere in the American tropics. It is closely related to the native *P. elsiae* Urban but may be distinguished from that and other native species by its drupaceous fruits and the common occurrence of staminodes in the female flower. Both *P. acidus* and *P. elsiae* belong to subg. *Cicca* (L.) Webster, which has perhaps been the most widely recognized of all segregates from *Phyllanthus*. However, subg. *Cicca* is related to some African species of subg. *Kirganelia* (Juss.) Webster, and it seems more convenient therefore to retain it with *Phyllanthus*.

Various other species of *Phyllanthus* may be cultivated in Panama, but the only one recorded seems to be *P. emblica* L., which resembles *P. acidus* in having drupaceous fruits; but these eventually dehisce, and the plant is easily distinguished from *P. acidus* by its much smaller linear-oblong leaves.

Useful reference:

Webster, G. L., A monographic study of the West Indian species of *Phyllan-*

thus. Jour. Arnold Arb. **37:** 91-122, 217-268, 340-359, 1956; **38:** 51-80, 170-198, 295-373, 1957; **39:** 49-100, 111-212, 1958.

a. Monoecious herbs; axes all persistent; leaves distichous, none reduced to scales (subg. *Isocladus*).
  b. Seeds minutely verruculose, ca 1 mm long or less; capsules ca 2 mm broad or less.
    c. Filaments of stamens free; stems terete, at most narrowly winged .....1. *P. caroliniensis*
    cc. Filaments of stamens united; stems compressed and distinctly winged .....2. *P. compressus*
  bb. Seeds smooth, 1.5 mm long or more; capsules ca 3 mm broad ....3. *P. hyssopifolioides*
aa. Monoecious or dioecious herbs, shrubs, or trees; leaves on persistent axes reduced to scales, developed leaves and flowers present only on deciduous branchlets.
  d. Dioecious shrubs or trees; cauliflorous; calyx-lobes and stamens usually 4, carpels usually 3, fruits with 1 or 2 developed cells, each with a single seed, pithy and indehiscent (subg. *Cicca*) .....4. *P. elsiae*
  dd. Monoecious, habit various, not cauliflorous (flowers axillary on deciduous branchlets); calyx lobes 5 or 6, stamens 3 (seldom 2); carpels usually 3, fruit capsular, dehiscent, each cell with 2 seeds.
    e. Branchlets pinnatiform; plants woody or herbaceous; pollen grains reticular, colporate (subg. *Phyllanthus*).
      f. Leaf-blades hispiduous beneath; ♀ flower subsessile; ovary distinctly roughened; seeds transversely ribbed .....5. *P. urinaria*
      ff. Leaf-blades smooth; ♀ flower definitely pedicellate; ovary smooth or nearly so; seeds striate or verruculose.
        g. Leaf-blades usually oblique at the base; stipules narrow, 2 mm long or more; ♂ calyx-lobes 1.2 mm long or longer; pollen grains 4-colporate; seeds verruculose, 1.4-1.8 mm long .....6. *P. niruri*
        gg. Leaf-blades not oblique; stipules not over 1.3 mm long; ♂ calyx-lobes less than 1 mm long; pollen grains 3-colporate; seeds striate or ribbed, 0.8-1.3 mm long.
          h. Cymules bisexual (1 ♂ and 1 ♀ flower); ♀ calyx-lobes narrowly obovate, 1 mm long or less, distinctly pointed at the tip; seeds with usually 5 or 6 distinct ribs .....7. *P. amarus*
          hh. Cymules unisexual; ♀ calyx-lobes broady obovate, rounded at the tip, 1.4 mm long or more (in fruit); seeds with ca 10-12 delicate striae.
            i. Filaments completely united, staminal column 0.25-0.4 mm high; pistillate disc angled or 5-lobed; seeds 1.1-1.3 mm long; stems sometimes thickened with aerenchyma below, leaves not narrowed towards tip .....8. *P. stipulatus*
            ii. Filaments only partially united, staminal column ca 0.1 mm high; pistillate disc divided into 3 narrow segments; seeds 0.9-1 (-1.1) mm long; stems never thickened with aerenchyma, leaves narrowed towards the tip .....9. *P. caribaeus*
    ee. Branchlets bipinnatiform; plants woody; pollen grains echinulose (subg. *Conami*).
      j. Leaf-blades abruptly caudate-pointed, scabrous-roughened above; pedicel of ♀ flower scabridulous, 5-14 mm long; seeds 2.5-2.8 mm long .....10. *P. acuminatus*
      jj. Leaf-blades evenly narrowed to an acute or obtuse tip, smooth; pedicel of ♀ flower smooth, 10-15 mm long; seeds 2.2-2.4 mm long .....11. *P. anisolobus*

1. **Phyllanthus caroliniensis** Walter, Fl. Carol. 228, 1788.

Herb, annual or short-lived perennial, ca 1-3 dm high; monoecious, branches terete or narrowly winged; stems unbranched to pinnately branched. *Leaves* membranous to firm; petioles short, 0.5-1 mm long; stipules auriculate, 0.7-2 mm long; blades elliptic to obovate, obtuse to rounded or apiculate, 5-20 mm long and 2-10 mm broad, paler beneath, the reticulum of veinlets often distinct. *Cymules* with usually 1 or 2 staminate and 1 or 2 pistillate flowers. *Staminate flowers* with (5-) 6 calyx-lobes, 0.5-0.7 mm long; disc-segments 6; stamens 3, the filaments free, short, the anthers opening horizontally; pollen grains oblong, 4-colporate. *Pistillate flowers* with pedicels sharply reflexed, 1 mm long or less; calyx-lobes usually 6, 0.6-1.4 mm long, linear to oblong; disc entire or dissected; ovary usually smooth, the styles bifid, less than 0.5 mm long. *Capsules* 1.6-2 mm in diam; seeds 0.7-1 mm long, dull grayish-brown, verruculose.

Latitudinally the most widespread species of *Phyllanthus,* extending from Pennsylvania south to Argentina, and showing marked geographic variation. The Panamanian specimens appear to represent two subspecies:

1a. **Phyllanthus caroliniensis** subsp. **caroliniensis.**

Stems terete or flattened, not distinctly winged, usually with a number of lateral branches; plants of relatively weedy habitats.

CANAL ZONE: Ancon, *Pittier 2761* (US); Balbo, *Standley 28558* (US), *29289* (US). DARIEN: El Real, *Burch et al. 1057* (MO). PANAMA: hills betw Capira & Potrero, *Dodge & Hunter 8618* (MO); Taboga I, *Standley 27832* (US, GH).

1b. **Phyllanthus caroliniensis** subsp. **stenopterus** (Muell.-Arg.) Webster, Jour. Arnold Arb. **37:** 348, 1956.

P. stenopterus Muell.-Arg. in DC., Prodr. **15**(2): 399, 1866.

Stems terete, sharply and narrowly (ca 0.1 mm wide) winged, unbranched to copiously branched; plants of wet situations.

CANAL ZONE: Chagres, *Fendler 273* pro parte (GH, NY, US); Fort Clayton to Corozal, *Standley 29043* (US). CHIRIQUÍ: David airport, *Lewis et al. 731* (GH, MO). PANAMA: vic of Chepo, *Pittier 4610* (US), *4661* (US); Las Sabanas, *Bro. Heriberto 147* pro parte (US); Race Track, Panama, *Standley 27757* (US); Punta Paitilla, *Standley 26236* (US); R.o Tocumen, *Standley 26607* (US); San José I, *Erlanson 443* (GH), *Harlow 78* (GH), *Johnston 185* (GH).

2. **Phyllanthus compressus** H.B.K., Nov. Gen. Sp. Pl. **2:** 109, 1817.

Herb, annual or short-lived perennial, up to ca 3 dm high, sparsely to freely branching; monoecious; branches distally flattened and with a sharp wing 0.2-0.25 mm across on each side, ca 1-1.2 mm wide (including wings only 0.7 mm or more wide on secondary branches). *Leaves* firm in texture; petioles usually less than 1 mm long; stipules auriculate, acuminate, ca 1-2 mm long; blades elliptic, obtusely but distinctly pointed, mostly 6-15 mm long and 2.5-5 mm broad, the primary veins sometimes distinct but not prominent, the secondary veins (and

sometimes all venation) obscure or invisible. *Cymules* with usually 1 or 2 ♂ and 1 or 2 ♀ flowers. *Staminate flowers* with pedicels usually less than 1 mm long; calyx-lobes usually 5, ca 0.5-0.7 mm long and broad; disc-segments 5, entire; stamens 3, the filaments united about halfway (sometimes less), less than 0.5 mm long, the anthers opening ± horizontally; pollen grains oblong, 4-colporate. *Pistillate flowers* with pedicels sharply reflexed, less than 1 mm long; calyx-lobes usually 5, ca 0.6-0.8 mm long, obovate; disc annular, entire; ovary smooth, the styles free, bifid, less than 0.4 mm long. *Capsules* ca 1.7-2 mm in diam; seeds ca 0.9-1 mm long, brownish, verruculose.

Mexico to Peru, usually in rather moist places.

BOCAS DEL TORO: Changuinola Valley, *Dunlap* 359 (F, US); id., 10-15 mi inland from mouth of Changuinola River, *Lewis et al.* 888 (DAV, GH, MO, US). PANAMA: sandy places on rocky shore, Boquerón waterfall, Río Boquerón, *Steyermark & Allen 17234* (MO).

This species is related to *P. caroliniensis* and could easily be confused with *P. caroliniensis* subsp. *stenopterus*, which also has winged stems. However, the stems of subsp. *stenopterus* are terete, more delicate, and with wings narrower (ca 0.1 mm), and it also agrees with typical *P. caroliniensis* in its veiny leaves and free filaments of the male flowers. The leaves of *P. compressus* are thicker than those of *P. caroliniensis* and have a dull, leaden appearance which (when taken with the inconspicuous veins) is distinctive.

3. **Phyllanthus hyssopifolioides** H.B.K., Nov. Gen. Sp. Pl. **2:** 108, 1817.

P. monocladus Urban, Repert. Sp. Nov. **15:** 404, 1919.

Annual herb, erect, completely smooth and glabrous; monoecious; main stem unbranched or nearly so, 1-2.5 dm high, 0.5-1 mm in diam, terete below, flattened above and with thin narrow wings 0.1-0.15 mm broad. *Leaves* with petioles 0.5-0.8 mm long; stipules ovate-lanceolate, acuminate, basally auriculate, ± denticulate, 1.2-1.5 mm long; blades ovate to oblong or elliptic, obtuse-apiculate at tip, 6-12 mm long, 2.5-5 mm broad, the lateral veins obscure to distinctly visible. *Inflorescences* unisexual, sexes at separate axils, the staminate in few-flowered clusters, the pistillate solitary. *Staminate flowers* with pedicels less than 1 mm long; calyx-lobes 5, obovate to broader than long, 0.6-0.7 mm long, 0.6-0.9 mm broad; disc-segments 5, cuneate to orbicular, thin, ca 0.2 mm in diam; stamens 3, the filaments free, ca 0.15 mm long, the anthers subglobose, 0.25-0.3 mm broad, dehiscing obliquely. *Pistillate flowers* with geniculate pedicels, 1 mm long or less; calyx-lobes 6, obovate to oblong, obtuse to subacute, (0.8-)1-1.2 mm long; disc-segments 6, cuneate, entire; ovary smooth, the styles horizontal, bifid, the style-branches dilated and thickened, appressed to the ovary, less than 0.2 mm long. *Capsules* subglobose, olivaceous, ca 3 mm broad; seeds 1.6-1.7 mm long, smooth, dull brownish with yellow coating.

Savannas, apparently in wet places, in several disjunct neotropical areas (Dominican Republic, Trinidad, Panama, northern South America).

CHIRIQUÍ: vic of Boquete, Llanos Francia, 3300 ft, *Stern et al. 1161* (DAV, MO); COCLÉ: Penonomé, *Ebinger 1020* (MO).

The recent (1959, 1960) collection of a widely disjunct population of this species in Panama is rather surprising, but as the plant is rather inconspicuous (and perhaps ephemeral), it may have been overlooked. It should be sought in savanna areas in other provinces.

4. **Phyllanthus elsiae** Urban, Repert. Sp. Nov. **15:** 405-406, 1919.

Bush or tree, up to 15 m high, glabrous; dioecious; older twigs 5-15 mm thick sometimes with conspicuous lenticels; scale-leaves on permanent branches ± deciduous, blackish, indurate, ca 1.5 mm long. *Deciduous branchlets* 1-3 dm long, 1.3-1.8 mm thick, with ca 10-20 leaves, the median internodes ca 1-1.5 cm long. *Leaves* chartaceous; *petioles* 2.5-3.5 mm long; stipules lanceolate, blackish-brown, 0.8-1.2 mm long; blades mostly broadly elliptic to suborbicular, rather abruptly pointed, 3-5(-7) cm long, 2-4(-5) cm broad. *Thyrsiform inflorescences* naked, clustered on spur-shoots; staminate axes mostly 1.5-7 cm long, the cymules with 10-20 flowers; pistillate axes mostly 3-6 cm long, the cymules with 1-4 flowers. *Staminate flowers* with calyx-lobes 4, 1-1.7 mm long; disc absent; stamens usually 4, the filaments free, ca 0.25 mm, the anthers dehiscing vertically; pollen grains 3-colporate. *Pistillate flowers* with pedicels 1-3 mm long; calyx-lobes 4, 0.8-1.3 mm long; disc absent; ovary of 3 (rarely 2) carpels, the styles connate at base, distally bifid, 1.8-2.3 mm long. *Fruits* oblate-spheroidal, usually 3-celled, 5-8.5 mm high, 5.5-10.5 mm broad, obtusely lobed, indehiscent, the outer layer soft and pithy, the inner hard and bony, fertile carpels usually 1 or 2 per fruit, each with 1 seed; seeds flattened, smooth, pale brown, ca 3-4 mm long.

Low forests along lagoons and rivers, usually near sea-level, southern Mexico to northern South America.

CANAL ZONE: banks of Chagres River, *Johnston 1713* (GH), *Maxon 4797* (US); forest along Río Indio de Gatun, *Pittier 2776* (US).

The ecology and distribution of this interesting species, which is closely related to the commonly cultivated *P. acidus*, has been discussed in an earlier publication (Jour. Arnold Arb. **38:** 73-75, 1957). The tree is doubtless common along the estuaries of many rivers in Panama, as well as the other Central American countries. *Phyllanthus chacoensis* Morong of Argentina and Paraguay is even more similar than *P. acidus*, but differs in having invariably 2-celled fruits and shorter, broader styles. These few American species of subg. *Cicca* appear to be relicts of a very ancient distribution.

5. **Phyllanthus urinaria** L., Sp. Pl. 982, 1753.

Herb, usually annual, erect or procumbent, up to 5 dm high; monoecious; main stems 1-3 mm thick, subterete with narrow sharp ridges decurrent from nodes; scale-leaves on main axes scarious, 2-3 mm long. *Deciduous branchlets* mostly 5-10 cm long, 0.5-0.75 mm thick, with 20-35 leaves. *Leaves* with very short petioles; stipules unequal, the longer 0.8-1.5 mm long, lanceolate; blades

mostly 8-25 mm long, 2-6(-9) mm broad, linear to oblong-obovate, obtuse or mucronulate at the tip, marginally hispidulous beneath. *Cymules* unisexual, the proximal nodes with solitary female flowers, the distal nodes with cymules of 5-7 male flowers. *Staminate flowers* with calyx-lobes 6, less than 0.5 mm long; disc-segments 6, crenulate; stamens 3, the filaments completely fused into a column, the anthers dehiscing vertically; pollen grains 4-colporate. *Pistillate flowers* with pedicels 0.5 mm long or less; calyx-lobes 6, linear to lanceolate, dorsally hispidulous, 0.6-0.9 mm long; disc entire or crenulate; ovary conspicuously papillate, the styles connate, bifid at the tips. *Capsules* 2-2.2 mm in diam, scurfy or nearly smooth, often reddish-blotched; seeds 1.1-1.2 mm long, light brown, with 12-15 sharp tranverse ridges on back and sides and often with 1-3 deep pits on the sides.

Of Old World origin, now widely distributed in tropical regions; a weed in moist habitats.

BOCAS DEL TORO: Almirante, *McDaniel 5071* (MO); Changuinola, *Lewis et al. 800* (GH, MO, UC); Chiriquí Lagoon, *von Wedel 1095* (MO), *2552* (MO). CANAL ZONE: Fort San Lorenzo, *Burch et al. 1031b* (MO); Fort Sherman, *Duke 4371* (MO); Frijoles, *Standley 27632* (US), Cocoli Road, *Burch et al. 1400* (MO). CHIRIQUÍ: David airport, *Lewis et al. 732* (GH, MO, US). DARIEN: El Real, *Burch et al. 1062* (GH, MO, UC, US). PANAMA: San José I, *Johnston 899* (GH).

6. **Phyllanthus niruri** L., Sp. Pl. 981, 1753.

P. lathyroides H.B.K., Nov. Gen. Sp. Pl. **2:** 110, 1817.

Annual herb 1-5 dm high, glabrous; monoecious; main stem smooth, terete, ca 1-2.5 mm thick, scale leaves scarious, becoming brownish, 1.5-3 mm long, narrow and acuminate. *Deciduous branchlets* mostly 5-10 cm long, 0.3-0.5 mm thick, subterete, smooth, with ca 15-30 leaves. *Leaves* thin; petioles 0.4-0.7 mm long; stipules linear-lanceolate, unequal, the longer of each pair 2-2.7 mm long; blades mostly ovate or elliptic, ca 7-17 mm long, 3-9 mm broad, acute or subacute at the tip, conspicuously oblique at the base, often conspicuously paler beneath. *Cymules* unisexual, the proximal 2-12 nodes of branchlets barren or with cymules of 3-7 staminate flowers, the distal nodes with solitary pistillate flowers. *Staminate flowers* with pedicels 1.2-1.8 mm long; calyx-lobes 5 (rarely 6), obovate or obcuneate, mostly 1.2-1.5 mm long; disc-segments 5, more or less papillate; stamens 3, the filaments ca 0.6-1 mm long, free or united to ¾ their length in a column, the anthers dehiscing obliquely; pollen grains 4-colporate. *Pistillate flowers* with pedicels usually becoming 2.5-4.5 mm long; calyx-lobes 5, elliptic or obovate, obtuse or rounded at the tip, 1.5-2.7 mm long; disc patelliform, somewhat angled and thickened; ovary smooth, the styles free, ascending, bifid, 0.5-0.6 mm long, the branches capitate. *Capsules* smooth, stramineous, ca 3 mm in diam; seeds dark brown or fuscous, 1.4-1.8 mm long, verruculose.

One of the most widespread native American species, extending from central Texas south to northern Argentina.

CHIRIQUÍ: Quebrada Velo, *Woodson & Schery 244* (F, MO); Volcán Chiriquí, *Davidson 873* (GH, MO, US), *Pittier 3067* (US). PANAMA: Bella Vista, *Killip 3071* (US).

Most of the material from Panama which has been called *P. niruri* proves to be misidentified; the species appears to be comparatively rare, especially since it has not been collected in the Canal Zone. It is easily separated from the more common *P. amarus* and *P. stipulatus* by its verruculose rather than striate seeds, longer stipules, and larger distinctly ribbed female calyx.

7. **Phyllanthus amarus** Schum. & Thonn., Kongl. Danske Vidensk. Selsk. Skr. **4:** 195-196, 1829.

P. niruri var. *amarus* (Schum. & Thonn.) Leandri in Humbert, Fl. Madag. **111:** 73, 1958.

Annual herb, glabrous, erect, 1-5 dm high; monoecious; main stem smooth, terete, usually 1.5-2 mm thick; scale-leaves scarious, brownish, 1-2 mm long. *Deciduous branchlets* 4-12 cm long, ca 0.5 mm thick, subterete (never sharply winged), smooth or proximally roughened, with ca 15-30 leaves. *Leaves* thin; petioles 0.3-0.5 mm long; stipules lanceolate, 0.8-1.3 mm long; blades elliptic-oblong or somewhat obovate, mostly 5-11 mm long and 3-6 mm broad, rounded to apiculate at the tip, only slightly (if at all) inaequilateral at base, the margins smooth or obscurely roughened. *Cymules* mostly bisexual, the proximal 1 or 2 axils with staminate flowers, the other axils each with one staminate and one pistillate flower. *Staminate flowers* with pedicels 0.6-1.3 mm long; calyx-lobes 5 (rarely 6), ovate or elliptic, 0.3-0.6 mm long; disc-segments 5, entire; stamens 3 (rarely 2), the filaments connate into a column 0.2-0.3 mm high, the anthers dehiscing obliquely or horizontally; pollen grains 3-colporate. *Pistillate flowers* with pedicels becoming 1-2 mm long in fruit; calyx-lobes usually 5, obovate-oblong, acute or apiculate, becoming 0.9-1 mm long; disc flat, deeply 5-lobed, sometimes irregular; ovary smooth, the styles free, ascending, shallowly bifid, less than 0.2 mm long. *Capsules* smooth, stramineous, 1.9-2.1 mm in diam; seeds sharply trigonous, light brown, 0.9-1 mm long, with 5 or 6 straight parallel ribs on the back.

Probably native to America, but now a circumtropical weed.

CANAL ZONE: Balboa, *Standley 25280* (US), *25662* (US), *29255* (US); Barro Colorado I, *Shattuck 398* (F); Colón, *Piper 3878* (US); Culebra, *Pittier 4773* (US); Fort Randolph, *Standley 28595* (US); Fort San Lorenzo, *Burch et al. 1032* (GH, MO, UC, US); Fort Sherman, *Standley 30937* (US); Frijoles, *Standley 31471* (US); Gatun, *Standley 27315* pro parte (US); Mt Hope Cemetery, *Standley 28853* (US); Margarita Swamp, *Maxon & Valentine 7063* (US); Summit, *Standley 30086* pro parte (US). CHIRIQUÍ: David airport, *Lewis et al. 746* (GH, MO). PANAMA: sabanas N of Panama City, *Bro. Paul 529 pro parte* (US); San José I, *Johnston 1315* (GH, MO, US).

This weedy plant, the most widespread and abundant species of *Phyllanthus*, has until recently been confused with *P. niruri;* its complicated nomenclatural history has been reviewed elsewhere (Jour. Arnold Arb. **37:** 6-8, 1956; **38:** 313-315, 1957). It is easily distinguished from *P. niruri*, however, by its equilateral leaf bases, bisexual cymules, and ribbed instead of verruculose seeds. It is more easily confused with *P. stipulatus*, but that plant has unisexual cymules and broader, more rounded pistillate calyx-lobes.

8. **Phyllanthus stipulatus** (Raf.) Webster, Contr. Gray Herb. **176:** 53, 1955; Jour. Arnold Arb. **38:** 315, 1957.

Moeroris stipulata Raf., Sylva Tellur. 91, 1838.
Phyllanthus diffusus Kl. in Seemann, Bot. Voy. Herald 105, 1853.
P. aquaticus Wright, Anal. Acad. Ci. Habana **7:** 110, 1870.

Herb, erect, usually annual, 2-5(-10) dm high; monoecious; main stem 1-2 mm thick or up to 4 mm and becoming spongy when plant grows in water; scale-leaves 0.5-1 mm long, scarious. *Deciduous branchlets* mostly 2-6 cm long, often reddish-tinged, smooth or scabridulous, with ca 15-30 leaves. *Leaves* smooth or minutely scabridulous on 1 or both sides; stipules lanceolate, 0.5-1 mm long; blades ovate or suborbicular, ca 3-10(-13) mm long, 2-4(-6) mm broad, obtuse to subtruncate at the tip, not unequal at the base. *Cymules* unisexual, the proximal axils barren or with cymules of 3-10 staminate flowers, the distal axils with solitary pistillate flowers. *Staminate flowers* with pedicels 0.4-0.7 mm long; calyx-lobes usually 5, obovate to orbicular, 0.5-0.9 mm long; disc-segments 5(-6), entire or crenulate; stamens 3 (rarely 2), the filaments connate into a column 0.25-0.35 mm high, the anthers dehiscing ± horizontally; pollen grains 3-colporate. *Pistillate flowers* with pedicels becoming 1.5-2.5 mm long; calyx-lobes 5, obovate, becoming 1.4-1.8(-2) mm long and 0.8-1.3(-1.5) mm broad, obtuse or rounded; disc 5-angled or lobed, sometimes asymmetric; ovary smooth, the styles free, 0.2-0.3 mm long, bifid, the tips subcapitate. *Capsules* ca 2.4-2.5 mm in diam, obscurely rugulose; seeds sharply trigonous, 1.1-1.3 mm long, light brown, with ca 10-12 delicate longitudinal striae.

Widespread in tropical America, often in wet places and sometimes growing in shallow water.

BOCAS DEL TORO: *Carleton 271* (US). CANAL ZONE: Chagres, *Fendler 273* pro parte (MO, US); Fort Kobbe, *Johnston 1620* (GH). CHIRIQUÍ: El Boquete, *Davidson 525* (US), *Killip 3632* (US). COCLÉ: Penonomé, *Ebinger 1023* (MO). PANAMA: San José I, *Johnston 184* (GH), *1004* (GH); Chepo, *Hunter & Steyermark s.n.* (MO); Juan Díaz, *Killip 3096* (US), *Standley 26225* (US); Laguna de Portala, *Pittier 4640* (US); Las Sabanas, *Bro. Heriberto 147* pro parte (US); Matías Hernandez, *Standley 28888* (US); Nuevo San Francisco, *Standley 30761* (US); Pacora, *Allen 997* (MO), *Woodson et al. 733* (F, MO); Panama, *Standley 27808* (US); sabanas N of Panama City, *Bro. Paul 529* pro parte (US).

9. **Phyllanthus caribaeus** Urban, Symb. Ant. **5:** 382, 1908.

Annual herb; monoecious; main stem slender, erect, 1-3.5 dm high, 0.5-2 mm thick; scale-leaves 0.5-0.9 mm long, scarious. *Deciduous branchlets* mostly 3-7 cm long, smooth or minutely scabridulous, with ca 15-30 leaves. *Leaves* membranous, minutely scabridulous on both sides; petioles 0.3-0.4 mm long; stipules lanceolate, 0.5-0.8 (-1) mm long; blades elliptic to ovate-oblong (± narrowed towards the tip), apically obtuse, 4-8 mm long, 2-3.5 mm broad. *Cymules* unisexual, the staminate flowers several at proximal axils of branchlet, the pistillate flowers solitary and distal. *Staminate flowers* with pedicels 0.3-0.8 mm long; calyx-lobes 5, suborbicular, 0.4-0.6 mm long; disc-segments 5, glandular-crenate; stamens 3, the filaments ca 0.2-0.25 mm long, united below into a column, the

anthers 0.2-0.25 mm broad, dehiscing ± horizontally; pollen grains 3-colporate. *Pistillate flowers* with pedicels becoming 1.5-2 mm long; calyx-lobes 5, oblong to obovate, becoming 1.2-1.6 mm long in fruit, obtuse; disc dissected into 3 linear or lanceolate somewhat unequal segments 0.25-0.5 mm long; ovary smooth, the styles free, spreading, 0.25-0.3 mm long, bifid, the tips scarcely thickened. *Capsules* ca 2 mm in diam, obscurely rugulose; seeds 0.9-1.1 mm long, yellowish-brown, with ca 10 longitudinal striae and many fine cross-bars.

Lesser Antilles, northeastern South America, and Panama; a rather weedy species of moist or wet habitats.

CANAL ZONE: Balboa, *Standley 29274* (US); Cerro Gordo, *Standley 26034* (US); Fort San Lorenzo, *Burch et al. 1031a* (DAV, GH, MO, US); Gatun, *Standley 27315* pro parte (US); betw Gamboa & Cruces, *Pittier 3764* (US); summit, *Standley 30086* pro parte (US). PANAMA: lower cloud forest, 2-3 mi S of Goofy Lake, rd to Cerro Jefe, 2000-2200 ft, *Lewis et al. 248* (DAV, GH, MO, US); Las Sabanas, *Bro. Heriberto 147* pro parte (US); San José I, *Johnston 1004* (GH).

The recent discovery in Panama of this characteristically Lesser Antillean species is surprising, and represents a disjunction of at least 1000 miles. The Canal Zone collections suggest the possibility of a recent introduction, but the locality near Cerro Jefe on the other hand would seem to indicate indigenous status. The species may well have been overlooked simply because it so closely resembles *P. stipulatus*.

10. **Phyllanthus acuminatus** Vahl, Symb. 95, 1791; Webster, Jour. Arnold Arb. **38:** 364, 1957.

P. conami Sw., Prodr. 28, 1788 (pro parte, quoad descr.).

Shrub or small tree, 2-8 m high, sparsely branching; monoecious; branches of current year producing 3-6 deciduous branchlets; scale-leaves inconspicuous, pale, less than 2 mm long. *Deciduous branchlets* bipinnatiform (except for first of the season); primary axis 2-5 dm long, ca 2-3 mm broad, wing-angled, dorsally rough or hirsutulous, with ca 8-20 ultimate axes, each 5-20 cm long, with mostly 7-20 leaves. *Leaves* membranous to chartaceous; petioles adaxially roughened or hirsutulous, 1.5-3 mm long; stipules triangular, blunt, those on primary axis up to 1.3 mm long (somewhat smaller on ultimate axes), persistent, often reflexed; blades ovate or elliptic, lucid and scabridulous above, smooth beneath (except along veins), ca 2-4.5 cm long, 1-2.5 ca broad, abruptly and bluntly cuspidate-acuminate at the tip, usually obtuse at base. *Cymules* bisexual, on ultimate axes, with 5-20 staminate and a single pistillate flower. *Staminate flowers* with pedicels capillary, 3-4.5 mm long; calyx-lobes 6, biseriate, the outer narrowly oblong, ca 0.9-1 mm long, 0.4-0.6 mm broad, the inner rotund, ca 0.9-1.2 mm long and broad; disc segments 3, reniform, massive; stamens 3, the filaments connate into a short column 0.1-0.3 mm high, the anthers triangular-ovate, apiculate, dehiscing horizontally; pollen grains globose, with 3 short diorate colpi, pilate. *Pistillate flowers* with pedicels 5-12 mm long, slender, often angled, scabridulous at least below; calyx-lobes 6, biseriate, with narrow whitish margins, the outer

elliptic, 1.1-1.4 mm long, 0.5-0.9 mm wide, the inner broadly ovate, 1.5-1.7 mm long, 1-1.3 wide; disc cupuliform, massive, 3-lobed; ovary oblate, smooth, deeply sulcate, the styles free, flattened, spreading, 0.4-0.6 mm long, divided ¼ to ½ their length. *Capsules* 4.5-5 mm in diam, conspicuously veiny, the columella massive, ca 2 mm long; seeds plano-convex, ca 2.5-2.8 mm long, reddish-brown, smooth with epidermis foveolate, sometimes with a rudimentary caruncle.

The most widespread woody American species of *Phyllanthus*, ranging from Mexico (Baja California, Tamaulipas) south through the West Indies and South America to northern Argentina (Jujuy, Salta).

BOCAS DEL TORO: Water Valley, *von Wedel 870* (GH, MO), *996* (GH, MO), *1623* (GH, MO), *1789* (GH, MO), *2744* (GH, MO); Shepherd I, *McDaniel 5170* (MO). CANAL ZONE: Balboa, *Standley 25597* (US), *26488* (US); Barro Colorado I, *Aviles 69* (F), *940* (F), *Bailey & Bailey 343* (F, GH), *570* (F, GH), *Bangham 382* (A, F), *Ebinger 640* (MO), *Salvoza 877* (A), *Woodworth & Vestal 671* (A, F, MO); Cocoli, *Riley 132* (MO); Coco Solo, *Dwyer & Duke 7916* (MO); Culebra, *Pittier 2216* (US); Curundu, *Tyson 1039* (MO), *1313* (MO); Darien, *Standley 31647* (US); France Field to Catival, *Standley 30405* (US); Old Fort Lorenzo, *Piper 5921* (US); Fort Sherman Reservation, *Maxon & Valentine 6989* (US), *7002* (US); Gamboa, *Standley 28359* (US); Gatun, *Standley 27260* (US), *Hayes 99* (NY); nr Miraflores Lake, Chiva-Chiva trail, *Tyson 1399* (MO); Miraflores to Pedro Miguel, *Pittier 3970* (F, US); Road C-21, *Duke 5786* (MO); Summit, *Woodson et al. 765* (A, F, MO), *Standley 29587* (US). CHIRIQUÍ: Progreso, *Cooper & Slater 223* (F, GH); Río San Cristobal, 2 mi W of David, *Tyson 916* (MO). COCLÉ: wet llanos betw Aguadulce and Antón, *Woodson et al. 1212* (A, F, MO); betw Las Margaritas and El Valle, *Woodson et al. 1734* (A, F, MO); El Valle, *Dwyer 1840* (MO). COLÓN: Porto Bello, *Ebinger 117* (MO). PANAMA: Chilibre, *Dwyer 1036* (MO); camino de Las Sabanas, *Bro. Heriberto 204* (GH, US); savanna-like areas nr top of Cerro Campana, *Duke 5978* (MO).

11. **Phyllanthus anisolobus** Muell.-Arg. in DC., Prodr. **15**(2): 382, 1866.—Fig. 3.

P. pittieri Pax, Anal. Inst. Fis.-Geogr. Nac. Costa Rica **9:** 195, 1898; in Pittier, Prim. Fl. Costar. **2**(5): 327, 1900.
P. mexiae Croizat, Jour. Wash. Acad. Sci. **33:** 14, 1943.

Shrub or tree, 3-8 m high, glabrous; monoecious; branches pale brown, smooth, scale-leaves inconspicuous. *Deciduous branchlets* mostly bipinnatiform, the primary axis 2-3.5 dm long, obtusely or sharply angled, green, smooth, usually with 5-10 lateral axes, each 8-30 cm long with 10-20 leaves. *Leaves* thin; petioles smooth, 2-3 mm long; stipules triangular, 0.6-0.8 mm long, subpersistent; blades broadly elliptic, evenly narrowed to a blunt or subacute tip, obtuse at the base, ca 2-5 cm long, 1.3-2.5 cm broad, smooth on both sides. *Cymules* bisexual, on the lateral branchlet axes, ♀ solitary, ♂ several. *Staminate flowers* with pedicels 3-7 mm long; calyx-lobes 6, 1.7-2.2 mm long, biseriate, the outer oblong, ca 0.7-0.8 mm broad, the inner elliptic, 1.2-1.8 mm broad (rarely lobes 5 and then subequal); disc of 6 massive rounded segments united by pairs into reniform glands ca 0.8 mm wide; stamens 3, the filaments connate into a column 0.8-1.2 mm high, the anthers deflexed atop the column, very deeply emarginate (anther-sacs stipitate), ca 0.4-0.5 mm in diam; pollen grains 3-colporate, reticulate. *Pistillate flowers* with smooth pedicels becoming 6-13 mm long; calyx-lobes 6, biseriate as in the ♂ flowers; disc of 6 segments united by pairs as in ♂, these 3 reniform glands usually confluent to produce a 3-lobed cup; ovary smooth, the styles 0.7-1.1 mm long, erect or

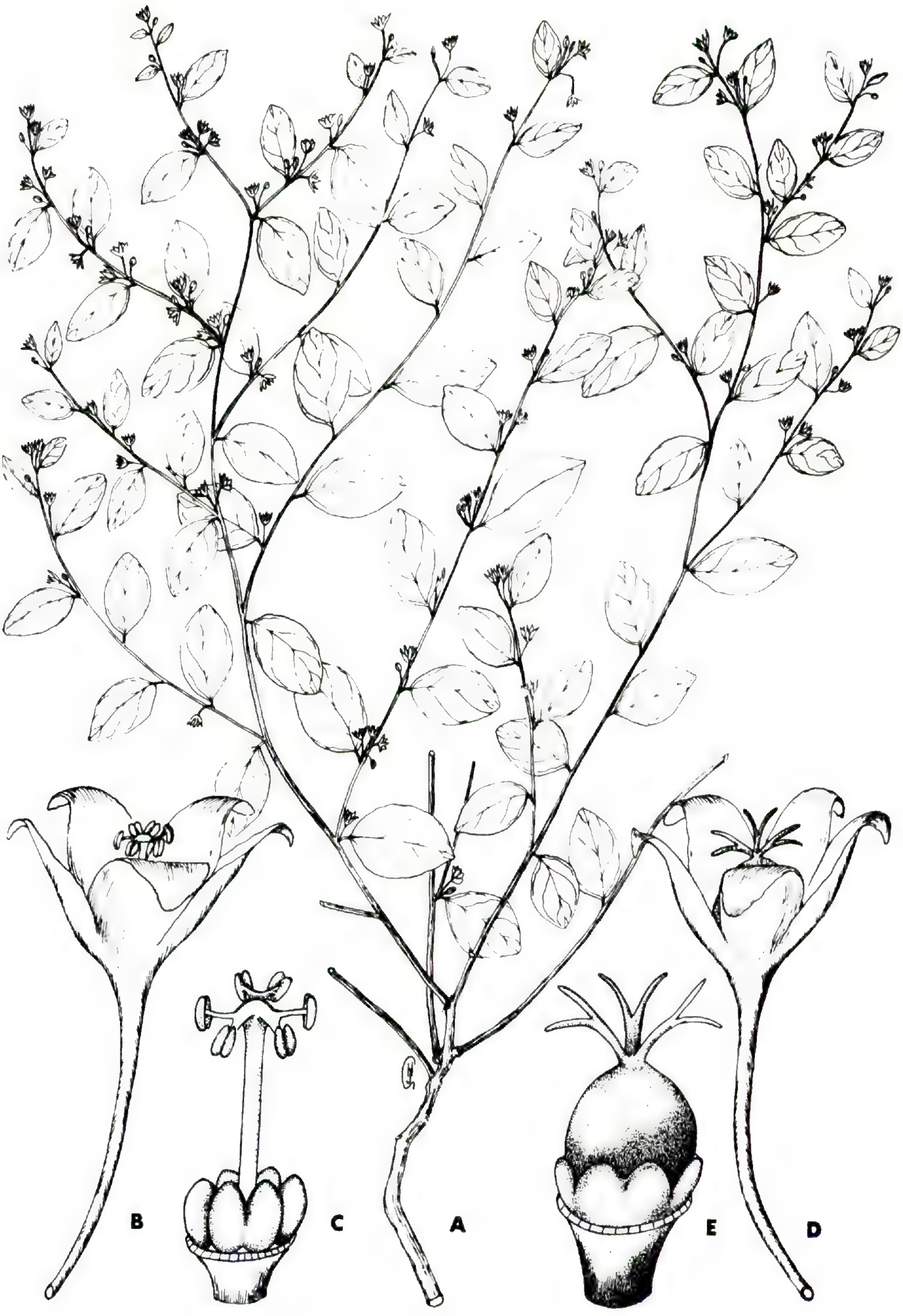

Fig. 3. *Phyllanthus anisolobus* Muell.-Arg.: A, habit (ca ×½); B, male flower (ca ×8); C, male flower with sepals removed (ca ×16); D, female flower (ca ×8); E, female flower with sepals removed (ca ×16). After *Lewis et al. 1802* (MO).

ascending, bifid, the branches slender. *Capsules* ca 3 mm long; seeds mostly 2-2.4 mm long, pale brown, smooth with slightly raised reddish swellings, sometimes with a rudimentary caruncle.

Rainforest areas, often along streams, at lower altitudes (below 1000 m), Costa Rica to Colombia and Peru.

COCLÉ: along streams, vic of Finca Tomas Arias, El Valle de Antón, 600 m, *Allen 3626* (F, MO, NY; hills N of El Valle de Antón, *Lewis et al. 1802* (MO).

The recent collection of good flowering material of the plant at El Valle shows clearly that the species represented is *P. anisolobus*, which was described from a Peruvian specimen of Pavon. Furthermore, its agreement in vegetative characters with the Costa Rican *P. pittieri* indicates that that species is synonymous with *P. anisolobus*. Pax's description of *P. pittieri* as having 5 calyx-lobes appears to be misleading, as all Costa Rican specimens which otherwise agree with his description have 6-merous calyces; apparently he happened to dissect one of the rare staminate flowers with 5 calyx-lobes. In the Costa Rican, Panamanian and South American plants of this affinity there is a strong resemblance in the flowers which marks *P. anisolobus* as distinct: the deeply emarginate anthers, with each anther-sac distinctly stipitate, are especially characteristic and set the species apart from all other taxa in subg. *Conami*.

A collection from Darien (La Palma, *Pittier 6600*, US) may also represent this species, but the specimen lacks pistillate flowers and is not positively identifiable. It differs mainly in having simply pinnatiform branchlets with only 5-10 leaves; however, most species in subg. *Conami* may produce a few pinnatiform branchlets before the characteristic bipinnatiform ones. Additional collections from La Palma are needed to resolve the status of the population there.

4. HYERONIMA

Hyeronima Fr. Allemão, Dissert. Pl. Nov. Brasil, 1848; Arch. Palestra Sci. Rio Janeiro **1:** 56, 1851.

Stilaginella Tul., Ann. Sci. Nat., Bot., sér. 3, **15:** 240, 1851.
Antidesma sect. *Hieronyma* Baillon, Hist. Pl. **5:** 243, 1874.

Trees or shrubs; dioecious; lepidote indumentum on all parts (except in *H. ferruginea*). *Leaves* alternate, entire; petiolate; stipules small or large, deciduous. *Inflorescences* axillary, racemose (sometimes almost spicate), usually aggregated into panicles; bracts inconspicuous; flowers with calyx a shallowly lobed cup; apetalous; disc well developed. *Staminate flowers* on very short pedicels; disc a rather massive cup, subentire or variously lobed; stamens 3-6, inserted within the disc, the filaments free, projecting beyond the calyx at anthesis, the anthers with an enlarged connective, introrse in the bud, the two anther-sacs pendant and divergent at anthesis, dehiscing longitudinally; pollen grains prolate, 3-colporate, psilate. *Pistillate flowers* shortly pedicellate; disc cupuliform, subentire, more tenuous than in the ♂; ovary ovoid, lepidote, the styles very short or not developed,

the bifid punctiform stigmata sessile, the carpels 2 with 2 ovules per locule. *Fruits* drupaceous, thin-walled, 1-celled, usually 1-seeded; seeds not carunculate, endosperm present, the cotyledons broader than the radicle, plane.

A stenomorphic genus restricted to the tropical portions of the New World. About 30 species have been recognized, but all are closely related and the genus badly needs a careful taxonomic revision. *Hyeronima* is the neotropical counterpart of the gerontogean genus *Antidesma*, which has very similar floral structure. Although *Hyeronima* seems sufficiently distinct by virtue of its lepidote indumentum and unilocular fruit, the flowers of the two genera are so similar that Baillon's combining them is understandable.

The Central American species of *Hyeronima* are poorly understood. Standley (Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 610, 1937) recognizes 4 species, all present in Costa Rica. However, all the Panamanian collections available so far appear to belong to the single following species.

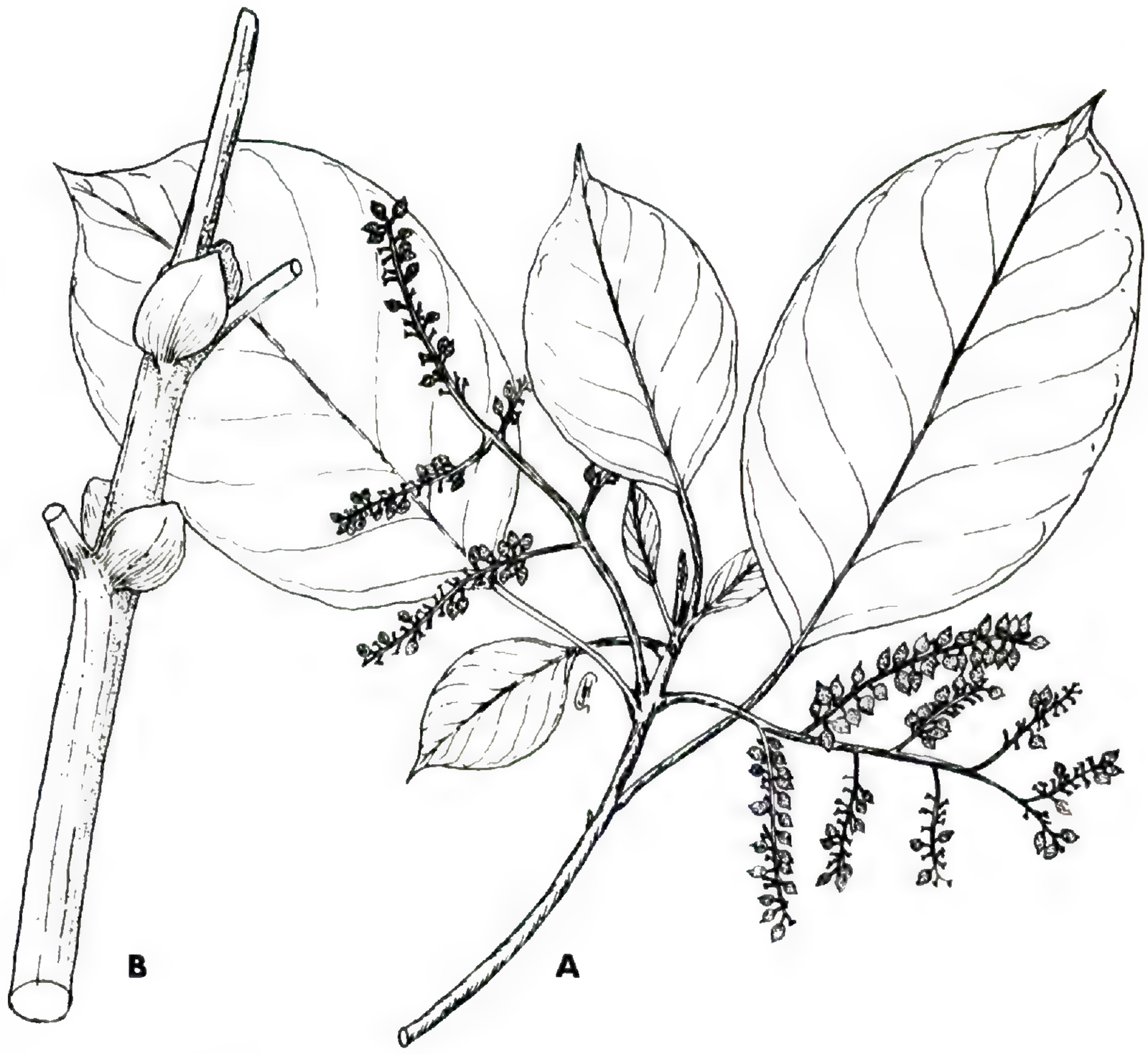

Fig. 4 *Hyeronima laxiflora* (Tul.) Muell.-Arg.: A, habit (ca ×½); B, stalk showing large stipules (ca ×½). A after *Carpenter* 57 (F); B after *Johnston 1798* (GH).

1. **Hyeronima laxiflora** (Tul.) Muell.-Arg., Linnaea **34:** 67, 1865.—Fig. 4.

Stilaginella laxiflora Tul., Ann. Sc. Nat., Bot. Sér. 3, **15:** 244, 1851.
? *Hieronyma caribaea* Urban, Repert. Sp. Nov. **16:** 139, 1919.

A tall *tree* up to 40 m high and over 1 m in diam with buttresses up to 1 m high or more; twigs subterete, angled, rather densely clothed, with orbicular peltate serrate-margined scales 0.1-0.2 mm in diam. *Leaves* on flowering twigs smooth or slightly roughened above, sparsely lepidote on both sides (densely so when young); petioles (2-)3-9 cm long; stipules stalked, deciduous, lanceolate, 5-15 mm long, 1-4 mm broad (stipules inflated and leaves much larger on sucker shoots); blades generally broadly elliptic, ca 10-30 cm long, 5-19 cm broad, rather abruptly acuminate, obtuse to rounded at the base, the major veins ca 8-11 on a side, straight, at nearly a 45° angle, impressed above, salient beneath, the veinlets evident but often not conspicuous beneath. *Panicles* densely lepidote, ♂ ca 9-17 cm long, ♀ 4-10 cm long; bracts on main axis resembling stipules; lateral axes mostly 4-6, unbranched, with minute bracts (less than 1 mm long). *Staminate flowers* with rigid pedicel ca ½ mm long; calyx cupuliform, shallowly and obscurely 3- or 4-dentate, densely lepidote; disc massive, ca as high as the calyx, subentire, fringed at the top with scaly hairs; stamens usually 4, the filaments elongating at anthesis to 0.6-0.8 mm or more, the anthers 0.4-0.5 mm long including the enlarged glandular connective; pistillode cylindric, ca 0.7-0.8 mm high, distally bifid, hirsutulous and with scaly trichomes. *Pistillate flowers* with stout pedicel, becoming 1.3-2 mm long in fruit; calyx similar to the ♂, becoming ca 0.5-0.8 mm high; disc shallower and much thinner than in the ♂, subentire, minutely pubescent along the rim; ovary ovoid, nearly 1 mm high, covered with peltate scales, the styles obsolete, the stigmas very small, punctiform, bifid. *Drupe* whitish, with an ellipsoidal bullate endocarp (2.5-)2.7-3.1 mm long and 2.4-2.6 mm in diam; seeds smooth, brownish, slightly over 2 mm long.

Rainforest at low altitudes, Panama to the Guianas.

BOCAS DEL TORO: Cricamola Valley, *Cooper 537* (F, NY). CANAL ZONE: Barro Colorado I, *Aviles 26* (F), *Bailey & Bailey 661* (F), *Carpenter 57* (F), *Shattuck 417* (F), *Standley 40863* (US), *41108* (US), *Woodworth & Vestal 643* (A), *701* (A), *Zeteck Z-5077* (F); Limon Bay, *Johnston 1798* (GH); Old Fort Lorenzo, *Piper 5989* (US). CHIRIQUÍ: Progreso, *Cooper & Slater 190* (F, NY, US), *209* (F, NY, US), *271* (F, NY, US); vic of San Felix, *Pittier 5461* (GH, NY, US). DARIEN: Caná, *Pittier 6970* (NY, US); Pidiaque, *Duke 8063* (MO). PANAMA: Río Tapia, *Standley 28178* (US).

The description is based on the Panamanian specimens only, and it is not certain that the plants really belong in the same species as *Hyeronima laxiflora* from the Guianas. Standley (Contr. U. S. Nat. Herb. **27:** 233, 1928) reported the plants from the Canal Zone as *H. alchorneoides* Fr. Allemão; that species is very similar to the Panamanian plants in its small fruit and other floral characters, but differs in having larger flowers (calyx 1 mm high or more) with a more massive pistillode (ca 0.4-0.5 mm across the truncate end vs. ca 0.2 mm across the ± notched end of the more slender pistillode of *H. laxiflora*). The species of *Hyeronima* are all so closely related, however, that it is difficult to draw any clear lines. From the geographic distribution alone, one would expect the Panamanian

plants to belong to *H. oblonga* (Tul.) Muell.-Arg. var. *benthamii* (Tul.) Muell.-Arg., which is cited from Mexico and Costa Rica by Pax and Hoffmann [Pflanzenreich **81** (IV, 147, XV): 38, 1922]. However, that plant (as represented in Costa Rica) differs in its larger calyx, glabrous ovary and divided male disc.

Part of the taxonomic difficulty in *Hyeronima* may be due to a considerable amount of vegetative plasticity. Some specimens (e.g. *Johnston 1798, Standley 30315*) have very large leaves up to 4 dm long or more and conspicuous cucullate stipules much broader (ca 1 cm or more) than usual. Such specimens appear to have been taken from saplings or sprout-shoots, and the leaves and stipules on reproductive twigs are never of such overgrown proportions. While it is not impossible that the Panamanian collections at hand may represent more than one species of *Hyeronima*, this is not proven, and it seems more probable that we are dealing with one variable taxon.

5. JATROPHA

Jatropha L., Sp. Pl. 1006, 1753; Gen. Pl. ed. 5, 437, 1754.

Curcas Adans., Fam. Pl. **2:** 356, 1763.

Trees, shrubs, or perennial herbs; monoecious or dioecious; stems with pale to distinctly colored latex. *Leaves* alternate, simple to lobed or divided, entire to conspicuously serrate; stipules often glandular or spinose. *Inflorescences* axillary or terminal, usually distinctly pedunculate, dichasial, ♀ flowers at proximal dichotomies and fewer than the ♂. *Staminate flowers* with 5 sepals, ± imbricate; petals 5, imbricate, free or coherent to connate, greenish or white to red; disc entire or dissected into segments; stamens mostly 8-12, the filaments connate, the anthers usually in 2(-6) whorls, dehiscing longitudinally; pollen grains globose, inaperturate, exine with massive hexagonal processes; pistillode reduced or absent. *Pistillate flowers* with 5 sepals, imbricate; petals as in ♂; disc annular or dissected; ovary of usually 3 carpels (rarely 2, 4, or 5), smooth, the ovules 1 per locule, the styles connate below or free, entire or bifid. *Fruits* capsular (but sometimes tardily dehiscent); seeds carunculate, with thin crustaceous testa, endosperm present, copious, the cotyledons broad, palmatinerved, the radicle short.

A pantropical genus of perhaps 150 species, with about 70-80 represented in America; only one species (*J. gossypiifolia*) is native in Panama. In addition to the three species enumerated below, various others are doubtlessly cultivated in gardens and may possibly be found escaped. *Jatropha podagrica* Hooker was described from Panama on the basis of a Seemann collection, but the original description makes it clear that this was a cultivated specimen; no indigenous Panamanian plants of the species have ever been discovered. From the Panamanian species described below, *J. podagrica* may easily be distinguished by its long-petioled peltate leaves, which are glaucous underneath.

Useful references:

McVaugh, R., The genus *Jatropha* in America: principal intrageneric groups. Bull. Torrey Bot. Club **72:** 271-294, 1945.

Wilbur, R. L., A synopsis of *Jatropha,* subsection *Eucurcas,* with the description of two new species from Mexico. Jour. Elisha Mitchell Soc. **70:** 92-101, 1954.

a. Stipules glandular-dissected; leaf-blades deeply 3-5-lobed, with marginal glandular teeth; petals dark purplish-red, glabrous; stamens mostly 8 ....1. *J. gossypiifolia*

aa. Stipules entire or obscure, not glandular; leaf-blades entire to lobed half way to midrib, without marginal glandular teeth; petals paler, hirsutulous; stamens mostly 10.

b. Petals small (less than 1 cm long), greenish-yellow, hirsutulous over most of inner face; fruits semi-drupaceous, tardily dehiscent; leaf-blades mostly deeply or broadly cordate at base, coarsely lobed, with 5-7 major veins at base .....2. *J. curcas*

bb. Petals larger (more than 1 cm long), bright red, hirsutulous only at base; fruits not fleshy, quickly dehiscent; leaf-blades rounded to narrowly cordate at base, entire or with small lateral or basal lobes, with 3-5 major veins at base .....3. *J. integerrima*

1. **Jatropha gossypiifolia** L., Sp. Pl. 1006, 1753.—Fig. 5.

J. staphysagrifolia Miller, Gard. Dict. ed. 8, 1768.

Subshrub or robust herb 1-2 m high, stems softly woody; branches glabrous. *Leaves* with petioles cylindric, 3-6 cm long, with branched glandular setae similar to those of the stipules; stipules parted to base into 2-4 slender branched glandulif-erous setae ca 3-5 mm long; blades 3-5-lobed halfway to the base or more, 5-8 cm long, mostly 7-15 cm broad, palmatinerved, ± cordate at base, the lobes oblong or elliptic, acute or short-acuminate at the tip, closely glandular-denticulate along margins, pinnately veined. *Dichasia* terminal on branches, with lateral axes alternate; peduncle minutely puberulent, ca 2-4 cm long; bracts lanceolate, acuminate, glandular-ciliate, the lower ones 8-12 mm long. *Staminate flowers* with pedicels less than 2 mm long; calyx-lobes ovate-lanceolate, acuminate, with stalked capitate glands on margins, distinctly imbricate, 2-4(-5) mm long; petals obovate, dark reddish or purplish-red, ca 3-5 mm long; stamens 8, the filaments 2.2-3 mm long, connate or strongly coherent in the lower ⅓, the anthers ovate, 0.5-0.7 mm long; pistillode absent. *Pistillate flowers* with pedicels less than 5 mm long, puberulent; calyx-lobes similar to staminate but puberulent and becoming larger (5-7 mm long); ovary pubescent, the styles slender, ca 1.5 mm long, dilated into emarginate stigmata. *Capsules* subglobose, 3-sulcate, ca 1 cm in diam, glabrescent, slightly verruculose; seeds dark grayish, with small black specks, mottled grayish- and brown, or dark chestnut brown, slightly compressed, 5.5-7.3 mm long, the caruncle massive, deeply laciniate, 1.2-1.9 mm long, 2.1-3.3 mm broad.

Wipespread in disturbed areas in tropical America; also introduced into the Old World.

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 2919* (MO); Isla Colón, *von Wedel 495* (MO). CANAL ZONE: Las Cruces trail, *Hunter & Allen 666* (MO). CHIRIQUÍ: El Boquete, *Pittier 3124* (US). HERRERA: Pesé *Allen 800* (MO); road from Chitré to Divisa, *Burch et al. 1366* (MO). LOS SANTOS: Playa de La Concepción, *Burch et al. 1260* (MO). PANAMA: Isla Taboga, *Woodson et al. 1529* (F, MO); nr beach at Nueva Gorgona, *Duke 4495* (MO).

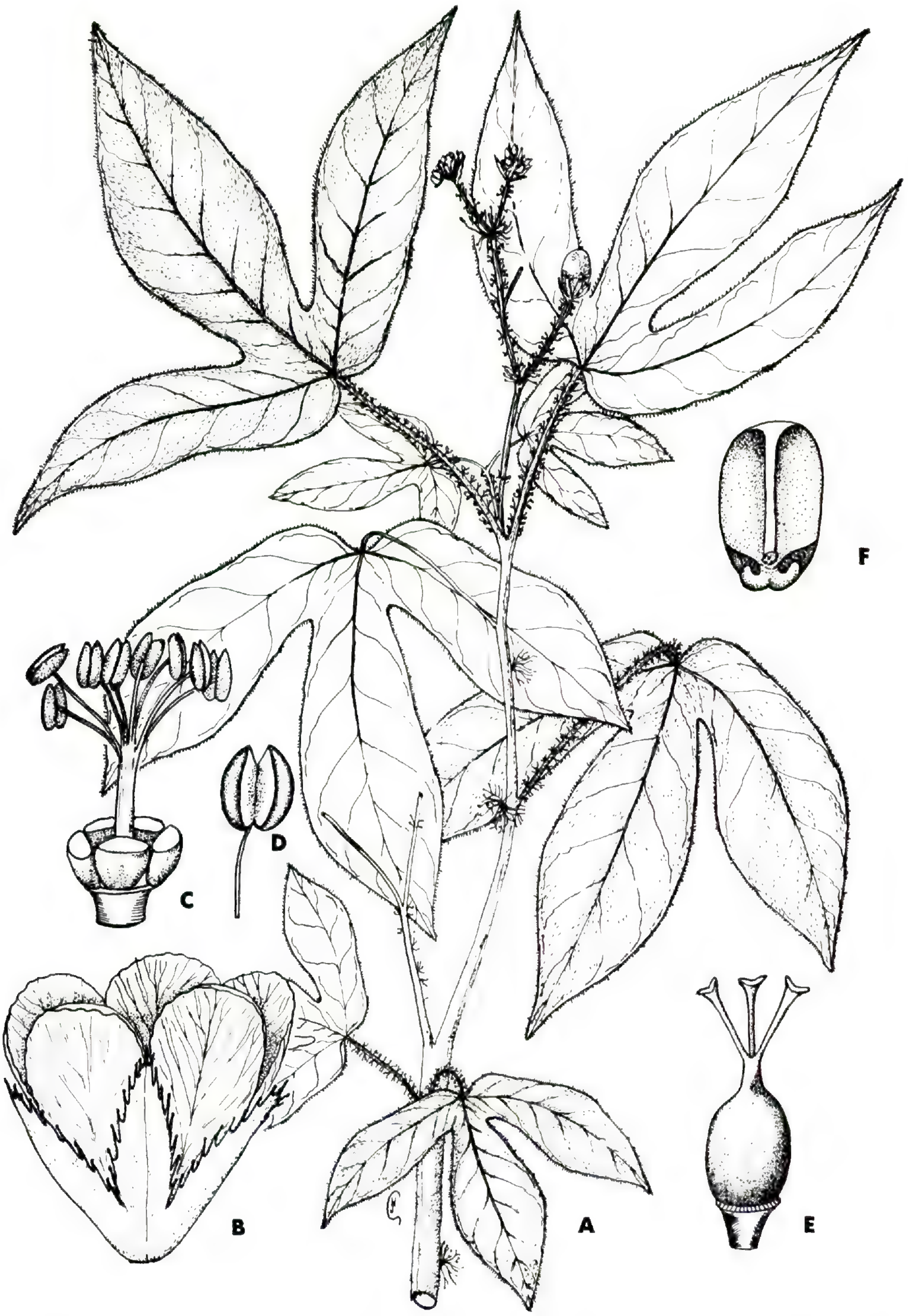

Fig. 5. *Jatropha gossypiifolia* L.: A, habit (×½); B, male flower (ca ×6); C, stamens (ca ×7); D, anther (ca ×10); E, female flower (ca ×10); F, seed (ca ×3). A after *Allen 800* (MO); B-D after *Burch et al. 1366* (MO); E after *Klug 3974* (MO), Peru; F after *Duke 4495* (MO).

2. **Jatropha curcas** L., Sp. Pl. 1006, 1753.

Shrub or small tree ca (1-) 2-5 m high; branches and mature foliage glabrous. *Leaves* with petioles (3-)9-15 cm long; stipules nearly obsolete, not evident on mature leaves; blades ovate, unlobed or coarsely (3-)5-7-lobed (lobes extending less than halfway to midrib), palmatinerved with mostly 7 nerves and deeply or broadly cordate at base, mostly 10-25 cm long, 9-15 cm broad, sparsely puberulent when young but soon glabrescent. *Dichasia* terminal on branches, bisexual or often unisexual; axes tomentulose, glabrescent, becoming ca 10-25 cm long; peduncles mostly 4-10 cm long; lower bracts narrowly lanceolate, 2-15 mm long, entire (not glandular). *Staminate flowers* with puberulent pedicels, ca 1-5 mm long, articulated below the flowers; calyx-lobes 5, elliptic, blunt, entire (not glandular), scarcely imbricate, ca 2.8-3.5 mm long; petals obovate, greenish or yellowish-white, adaxially hirsute, ca 5-6 mm long; disc-segments 5, ellipsoid, erect, massive, ca 1 mm high; stamens (8-)10, the filaments 2.2-3.7 mm long, connate below the middle, the anthers elliptic, 1-1.6 mm long; pistillode absent. *Pistillate flowers* with pedicels 5-9 mm long, up to 10-13 mm long in fruit, glabrous; calyx-lobes 5, oblong to lanceolate, foliaceous, obtuse or subacute at tip, entire, becoming ca 7-9 mm long; petals similar to the staminate; ovary glabrous, the styles slender, ca 1.5 mm long, connate in lower half, dilated into massive stigmata. *Capsules* ellipsoidal, ca 3 cm long and 2 cm broad, more or less fleshy, at length drying and dehiscent; seeds blackish, encrustate-striate, 15-22 mm long, distinctly beaked beyond the hilum, the caruncle appressed to the beak, not massive, deeply lobed, ca 2 mm long and 3.5 mm broad.

Native probably to Mexico and Guatemala; widely distributed throughout the tropics as a medicinal or hedge plant, and often escaping.

BOCAS DEL TORO: Isla Colón, *von Wedel 494* (MO). CANAL ZONE: betw Juan Mina & El Vigia, *Pittier 2400* (US). COLÓN: Giral, nr Bat Cave, *Blum & Tyson 518* (MO). DARIEN: 3 mi E of Santa Fé, *Tyson et al. 4657* (MO). HERRERA: Ocú, *Allen 4065* (MO). LOS SANTOS: Monagre beach rd, 5 mi SE Los Santos, *Lewis et al. 1682* (DAV, GH, MO, UC, US); Pocri, bridge over Río Purio, *Dwyer 2456* (MO); Playa de La Concepción, *Burch et al. 1258* (MO). PANAMA: Isla Taboga, *Woodson et al. 1509* (F); 1 mi E of Tocumen airport, *Blum & Tyson 1968* (MO).

3. **Jatropha integerrima** Jacquin, Sel. Stirp. Pl. Amer. 256, *t. 183 fig. 47*, 1763.

J. hastata Jacquin, loc. cit. *t. 173 fig. 54.*
J. pandurifolia Andr., Bot. Repos. **4**: *t. 267*, 1799.

Shrub ca 2-4 m high; branches and foliage glabrous or sparsely hirsutulous. *Leaves* entire or often with a pair of small acute lobes below the middle; petioles mostly 3-7 cm long; stipules nearly obsolete, not evident on mature leaves; blades ovate to elliptic, abruptly short-acuminate, palmatinerved with 5(-7) main veins at the rounded or subcordate base, 5-15 cm long, 2.5-8(-13) cm broad. *Dichasia* terminal or pseudo-axillary, often bisexual; peduncles ca 5-10 cm long; lower bracts lanceolate, mostly 2-5 mm long, entire or obscurely glandular-dentate. *Staminate flowers* with pedicels mostly 5-8 mm long, articulate near the top; calyx ca 2.5-3.5 mm long, lobed about halfway, the lobes blunt, entire, not imbricate; petals elliptic-obovate, bright red, adaxially hirsute at base (glabrous

over most of inner face), 15-22 mm long; disc-segments 5, rounded, reddish, ca 0.5-0.7 mm wide; stamens 10, the filaments ca 5-7 mm long, connate over halfway into a column, the anthers linear to oblong-lanceolate, mostly 2.5-3 mm long; pistillode absent. *Pistillate flowers* with pedicels becoming 5-9 mm long, glabrescent; perianth similar to the ♂; ovary glabrous, the styles ca 2.5 mm long, slender, bifid, the stigmata linear. *Capsules* subglobose-cylindric (truncate), trisulcate, ca 12-13 mm long and broad; seeds fuscous, mottled with dark specks, slightly compressed, 9.6-10 mm long, 5.1-5.8 mm broad, the caruncle bipartite, flabellate-laciniate, ca 2 mm long, 3 mm broad.

A polymorphic species native to Cuba, now extensively cultivated in gardens in the Caribbean area. According to at least one herbarium record (*Duke 8519*), the plant has become established in the wild, and it may be expected as a common escape.

CANAL ZONE: yards, Curundu, *Blum & Tyson 1075* (MO), *Tyson 2633* (MO), *4189* (MO). SAN BLAS: Isla Suskatupo, *Duke 8519* (MO).

6. GARCIA

Garcia Vahl in Rohr, Skriv. Naturh. Selsk. Kjöbenh. **2:** 217, *t. 9*, 1792.

Shrubs or trees; monoecious; latex scanty. *Leaves* alternate, entire; petiolate; exstipulate; pinnately veined. *Inflorescence* a terminal cluster (reduced cyme) with 1 or 2 pistillate and several staminate flowers; flowers with calyx perulate in bud, rupturing into 2 or 3 valvate segments; petals 6-13, narrow, sericeous, exceeding the calyx. *Staminate flowers* with persistent calyx; disc dissected into segments; stamens numerous (ca 30 to over 100), the filaments free; pollen grains globose, inaperturate, exine with massive hexagonal processes; pistillode absent. *Pistillate flowers* with stout pedicels; calyx deciduous; disc deeply lobed; ovary of 3 carpels, sericeous, the ovules 1 per locule, the styles short, thick, reflexed, bifid. *Fruits* capsular; seeds ecarunculate, the endosperm copious.

This small American genus includes only 2 species, the following and *G. parviflora* Lundell of eastern Mexico.

Useful reference:

Lundell, C. L., The genus *Garcia* Vahl, a potential source of superior hard quick-drying oil. Wrightia **1:** 1-12, 1945.

1. **Garcia nutans** Vahl in Rohr, Skriv. Naturh. Selsk. Kjöbenh. **2:** 217, *t. 9*, 1792.—Fig. 6.

Shrub or tree to 15 m high; twigs hispidulous to tomentulose. *Leaves* chartaceous to subcoriaceous; petioles 1-5 cm long; stipules absent; blades oblong to elliptic, abruptly acuminate to obtuse at the tip, obtuse to rounded at the base, mostly 8-19 cm long, 2.5-7 cm broad, sparsely to densely pilose beneath, the margins entire. *Staminate flowers* with hispidulous to densely pilose pedicels ca 1-3.5 cm long; calyx 6-13.5 cm long, tomentulose without; petals 6-13, linear to oblong-elliptic, pinkish to dark red, more or less hirsute, 10-17 mm long; disc-segments numerous, up to 1.5

Fig. 6. *Garcia nutans* Rohr: A, habit (ca ×½); B, male flower (ca ×4); C, anther (ca ×12); D, seed (ca ×1). A after *Matuda* 3568 (MO), Mexico; B-D after *Stern et al. 1872* (MO).

mm high, scattered over the pilose receptacle; stamens ca 60-150, the filaments mostly glabrous, ca 2.5-6 mm long, the anthers apiculate, 0.7-1 mm long. *Pistillate flowers* with tomentulose pedicels 1-3 cm long; perianth similar to the ♂; disc lobed, ca 2 mm high; ovary densely sericeous, the styles thick, 1.5-2 mm long, the stigmas fleshy, reddish to nearly black. *Capsules* 3-lobed, 3-seeded, 2-2.5 cm high, 3-4 cm in diam, sericeous; seeds globose, to 17 mm in diam.

According to Lundell, the species is native to eastern Mexico (San Luis Potosí to Chiapas), and other records represent escaped or cultivated plants. However, McVaugh (Brittonia **13:** 187, 1961) has reported a wild population from Jalisco, and the Panamanian collection cited below would also appear to represent a native plant. The species may prove to be indigenous over a wide area from southern Mexico to Colombia.

LOS SANTOS: scraps of forest betw Tonosí and Guánico, *Stern et al. 1872* (MO).

7. MANIHOT

Manihot Miller, Gard. Dict. ed. 4, 1754.

Trees, shrubs, or herbs, with milky latex; monoecious; roots often tuberous. *Leaves* alternate, long-petiolate, stipulate; blades mostly palmately lobed or divided, without distinct foliar glands. *Inflorescences* terminal (sometimes pseudo-axillary) panicles, the pistillate several on basal branches, the staminate ± racemose along the central axis; flowers with a 5-merous uniseriate perianth (petaloid calyx), petals absent. *Staminate flowers* with distinctly gamosepalous calyx, lobes imbricate in bud; disc central, intrastaminal, entire or 5-lobed, lobes ± bifid; stamens 10, biseriate, the outer opposite the calyx-lobes, the filaments free, the anthers introrse, dehiscing longitudinally; pollen grains globose, periporate, exine clavate; pistillode rudimentary or absent. *Pistillate flowers* long-pedicellate; calyx more deeply lobed than in staminate flowers; disc pulviniform, staminodia sometimes present; ovary of 3 carpels, smooth to ribbed or winged, the ovules 1 per locule, the styles connate below, the stigmata dilated to lacerate. *Fruits* capsular; columella often persistent; seeds carunculate, with thin crustaceous testa, endosperm copious, the embryo with broad palmately veined cotyledons.

Over 150 species have been described in this strictly American genus, most of them from Brazil. The species of *Manihot* are notoriously difficult to discriminate, and the total number may be considerably reduced when the genus is monographically revised. In addition to the two species enumerated below, at least one other, *M. glaziovii* Muell.-Arg. (the Ceará rubber tree of Brazil), may be found in cultivation. It is readily distinguished by its arboreal habit, peltate leaves, and larger fruits (2 cm in diam or more).

Useful reference:

Rogers, D. J., Studies on *Manihot esculenta* Crantz and related species. Bull. Torrey Bot. Club **90:** 43-54, 1963.

a. Leaves mostly with 7-9 lobes; ♂ calyces 12-14 mm long, glabrous within; ♂ disc ± entire; anthers glabrous; ovary not sharply ribbed or winged; seeds 7-9 mm broad ..... 1. *M. gualanensis*

aa. Leaves mostly with 3-5 lobes; ♂ calyces 3-4.5 mm long, pubescent within; ♂ disc 10-lobed; anthers apically puberulent; ovary (and fruit) sharply ribbed or winged; seeds 4-6.5 mm broad ..... 2. *M. esculenta*

1. **Manihot gualanensis** Blake, Contr. U. S. Nat. Herb. **24:** 13, 1922.—Fig. 7.

Shrub 1-4 m high, glabrous. *Leaves* with petioles ca 8-25 cm long; stipules linear-lanceolate, attenuate-acuminate, ± split into segments, ca 9-10 mm or more, soon deciduous; blades cut nearly to base with (5-)7-9 lobes, the lobes oblanceolate, abruptly short-acuminate, glaucous beneath, the middle lobe ca 10-15 cm long and 3-4 cm broad, the lateral lobes smaller. *Panicles* ca 2 dm long, with a few basal pistillate flowers and numerous staminate flowers above; flowers mostly on reflexed pedicels. *Staminate flowers* with pedicels 7-10 mm long; calyx broadly campanulate, somewhat inflated, yellowish- or greenish-white, ca 12-14 mm long, glabrous, the calyx-lobes 5-8 mm long, deltoid-oblong, obtuse-apiculate; disc massive, convex, ca 4 mm wide; stamens 9 or 10, the filaments to ca 7.5 mm long, glabrous, the anthers oblong or linear, 2.5-3 mm long, glabrous; pistillode absent. *Pistillate flowers* with pedicels becoming 5-15 mm long in fruit; ovary glabrous, not winged. *Capsules* ca 1.5 cm long, valves rugose; seeds plumply lenticular (somewhat more convex abaxially), grayish to pale brownish flecked with dark brown, 9-9.7 mm long, 7.5-9 mm broad, the caruncle deltoid, not very massive, subentire, 1.5-2 mm long, 3-3.6 mm broad.

Guatemala south to Panama.

CANAL ZONE: Upper Chilibre R, ½-1 mi below Chilibre, *Seibert 1506* (MO); Farfan Beach area, *Tyson 1837* (MO), *4108* (MO). DARIEN: vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 864* (DAV, MO); vic of Yaviza, along Río Chucunaque, edge of woods, *Stern et al. 101* (DAV, MO).

The identification of these Panamanian specimens as *M. gualanensis* Blake is accepted on the advice of the expert in the group, Dr. David J. Rogers, who kindly determined one of the Tyson specimens.

The collections from Darien are vegetative, and their identification as *M. gualanensis* is uncertain; additional collections of wild cassava plants in Panama are much needed in order to establish whether more than one species is present. Hemsley (Biol. Centr.-Amer. Bot. **3:** 121, 1883) cited *M. carthagenensis* (Jacquin) Muell.-Arg. from Panama on the basis of a specimen from Paraíso, Canal Zone (*Hayes 717*). Without examining the specimen, it is impossible to determine whether the collection is really that species rather than *M. gualanensis*.

2. **Manihot esculenta** Crantz, Inst. **1:** 167, 1767.

Jatropha manihot L., Sp. Pl. 1007, 1753.
Manihot utilissima Pohl, Pl. Brasil. Icon. Descr. **1:** 32, *t. 24*, 1827; Pax & Hoffm., Pflanzenreich **44** (IV, 147, II): 67, 1910.

Herb or shrub, sometimes arborescent, ca 1-3 m high, glabrous. *Leaves* with petioles 5-17 cm long; stipules lanceolate, acuminate, 7-8 mm long, deciduous; blades mostly deeply 3-5-lobed (less commonly 7-lobed, or sometimes undivided);

Fig. 7. *Manihot gualanensis* Blake: A, habit (×1); B, inflorescences (ca ×½); C, flower (ca ×2); D, stamen (ca ×10); E, seed (ca ×2). A-D after *Tyson 4108* (MO); E after *Tyson 1837* (MO).

lobes mostly elliptic-lanceolate, acuminate, glaucous beneath, the middle lobe ca 9-17 cm long, (1-)2-5 cm broad, the lateral lobes mostly smaller. *Panicles* 0.5-1 dm long at anthesis, lengthening in fruit; flowers on spreading or somewhat reflexed pedicels. *Staminate flowers* with pedicels 4-6 mm long; calyx campanulate, yellowish-green, ca 3-4.5 mm long, glabrous outside; calyx-lobes ca 2-2.5 mm long, deltoid, densely puberulent within; disc 10-lobed (i.e. of 5 concrescent bilobed segments), ca 2 mm wide; stamens 10, the filaments unequal, the longer not over 2 mm long, the anthers linear-oblong, 1.8-2 mm long, those on shorter filaments with apical tufts of hairs; pistillode absent. *Pistillate flowers* with pedicels 7-12 mm long, becoming ca 1.5-2 cm in fruit; calyx-lobes 5, oblong-lanceolate, acute, ca 7.5-10 mm long; disc massive, ca 3-3.5 mm wide; ovary with 6 sharp ribs or wings, the styles ca 1.8-2 mm long, dilated and divided into several capitate tips. *Capsules* ca 1.5 cm long, 1.3 cm in diam, rugose and 6-winged; seeds compressed, bluntly beaked, grayish or pale brownish, dark-flecked, 7.1-9.3 mm long, 4.1-5.1 mm broad, the caruncle broadly deltoid, entire, 1.3-1.7 mm long, 2.8-3.2 mm broad.

Apparently native to South America; widely cultivated in the tropics, including Panama, where the plant at least occasionally escapes.

BOCAS DEL TORO: Chiriquicito, *Seibert 1549* (MO). CANAL ZONE: Balboa, *Standley 25509* (US), *25559* (US), *25563* (US); Balboa, Sosa Hill, *Standley 25252* (US); Barro Colorado I, *Shattuck 161* (GH, MO); Cerro Gordo, *Pittier 2302* (US); Fort Randolph, swampy woods, *Standley 28637* (US); Río Pedro Miquel, *Standley 29930* (US). PANAMA: Taboga I, *Standley 27961* (US).

8. CNIDOSCOLUS

Cnidoscolus Pohl, Pl. Brasil. Icon. Descr. **1:** 56, 1827, nom. cons. prop.

Tree, shrubs, or herbs; monoecious; stems and leaves containing milky latex and armed with stinging hairs. *Leaves* alternate; petioles long, glandular at junction with blade; stipules usually present; palmately (rarely pinnately) veined, mostly palmately lobed, sometimes deeply parted and nearly compound. *Inflorescences* terminal (sometimes pseudo-axillary) dichasia, the pistillate flowers at the lower (proximal) nodes, the staminate at upper nodes; flowers with more or less petaloid calyx, usually white; apetalous. *Staminate flowers* with calyx gamosepalous, lobes imbricate in bud; disc annular; stamens 8-10(-25), the outer free and the inner connate (or all connate); pollen grains globose, periporate, clavate; filiform staminodes (pistillodes?) sometimes present atop staminal column. *Pistillate flowers* with calyx chorisepalous, the sepals deciduous (or gamosepalous in some species); disc annular, sometimes with staminodes; ovary of 3 (rarely 5) carpels, the ovules 1 per locule, the styles ± free, several times bifid or laciniate (rarely once bifid), sometimes apically dilated. *Fruits* capsular (rarely drupaceous); seeds carunculate, with copious endosperm, the embryo straight, the cotyledons broad and longer than radicle.

An American genus of about 50 species, the majority in Mexico and Brazil. Although earlier confounded with *Jatropha, Cnidoscolus* is much closer to *Manihot,* which it resembles in its apetalous flowers and periporate pollen grains. *Cnidos-*

colus is unique, however, in its armament of painfully stinging hairs. The single native species, *C. urens*, belongs to an herbaceous complex in sect. *Jussieuia* (Houst.) Pax & Hoffmann.

Useful reference:

McVaugh, R., The genus *Cnidoscolus*: generic limits and intrageneric groups. Bull. Torrey Bot. Club **71:** 457-474, 1944.

a. Herbaceous or only slightly woody, 0.5-2 m high; stems and leaves heavily armed with stinging hairs; leaves 3-5-lobed, lobes finely denticulate; petiolar gland of many small digitiform processes; pistillate flowers only 3-6 per inflorescence, sepals ca 3 mm long, styles incrassate ..... 1. *C. urens*

aa. Arborescent shrub or tree, mostly 3-8 m high or more; stems and leaves (except sometimes for petioles and leaf-veins) nearly unarmed; leaves mostly 7-lobed, lobes coarsely and sharply again lobed; petiolar gland entire; pistillate flowers up to 20-30 per inflorescence, sepals 5-7 mm long, style-tips very slender ..... 2. *C. aconitifolius*

1. **Cnidoscolus urens** (L.) Arthur, Torreya **21:** 11, 1921.—Fig. 8.

Jatropha urens L., Sp. Pl. 1007, 1753.
J. adenophila Pax & Hoffm., Pflanzenreich **63** (IV, 147, VII): 400, 1919.
Cnidoscolus adenophilus (Pax & Hoffm.) Pax & Hoffm., Naturl. Pflanzenfam. ed. 2, **19c:** 166, 1931.

Herb or softly woody subshrub 0.5-2 m high; stems densely armed with rigid stinging hairs 2-6 mm long. *Leaves* chartaceous; petioles mostly 3-12(-15) cm long, pubescent, sparsely to densely armed; junction of petiole and blade with a dense cluster (1.5-3 mm wide) of small digitiform glands; stipules split into a central subulate greenish part 2-5 mm long and several small lateral glands or gland-tipped setae; blades ovate or suborbicular in outline, 3-5-lobed, ± cordate at base, ca (5-)7-15 cm long, 8-18 cm broad, 5-7-palmatinerved, pubescent (often more densely so beneath), with stinging hairs along veins, the lobes oblong to obovate, obscurely to sharply denticulate, abruptly acute to acuminate. *Dichasia* terminal (or pseudoaxillary due to sympodial growth); peduncles sparsely to densely armed, 3.5-12 cm long; pistillate flowers ca 3-6 per inflorescence, at proximal axils; staminate flowers ca 10-25 per inflorescence, clustered at tips of second-order branches. *Staminate flowers* subsessile (pedicels to 1 mm long); perianth greenish-white, unarmed, oblong-urceolate in bud, ca 11-13.5 mm long (in Panamanian specimens); perianth tube cylindric, basally dilated, ca 3-7.5 mm long, unarmed, glabrous to densely pubescent, the lobes suborbicular to ovate or broadly elliptic, ca 3-6 mm long, rounded, unarmed or with 1 or 2 stinging hairs, moderately to densely pubescent without (rarely glabrous); disc pulviniform, closely adnate to the base of the staminal column, densely hispidulous, 1 mm wide or more; stamens 10, biseriate, the outer series with filaments free, ca 3.5-4 mm long, the inner series with filaments ca 6.5-8.0 mm long, connate more than halfway into a column, the anthers elliptic, 1.3-1.5 mm long; staminodes filiform, ca 1.5-2.5 mm long. *Pistillate flowers* nearly sessile, pedicels becoming 1-4 mm long in fruit; sepals distinct, whitish, oblong, caducous, 2.8-3 mm long; disc a small annular ring ca 0.2 mm high; ovary pubescent and usually armate, sometimes

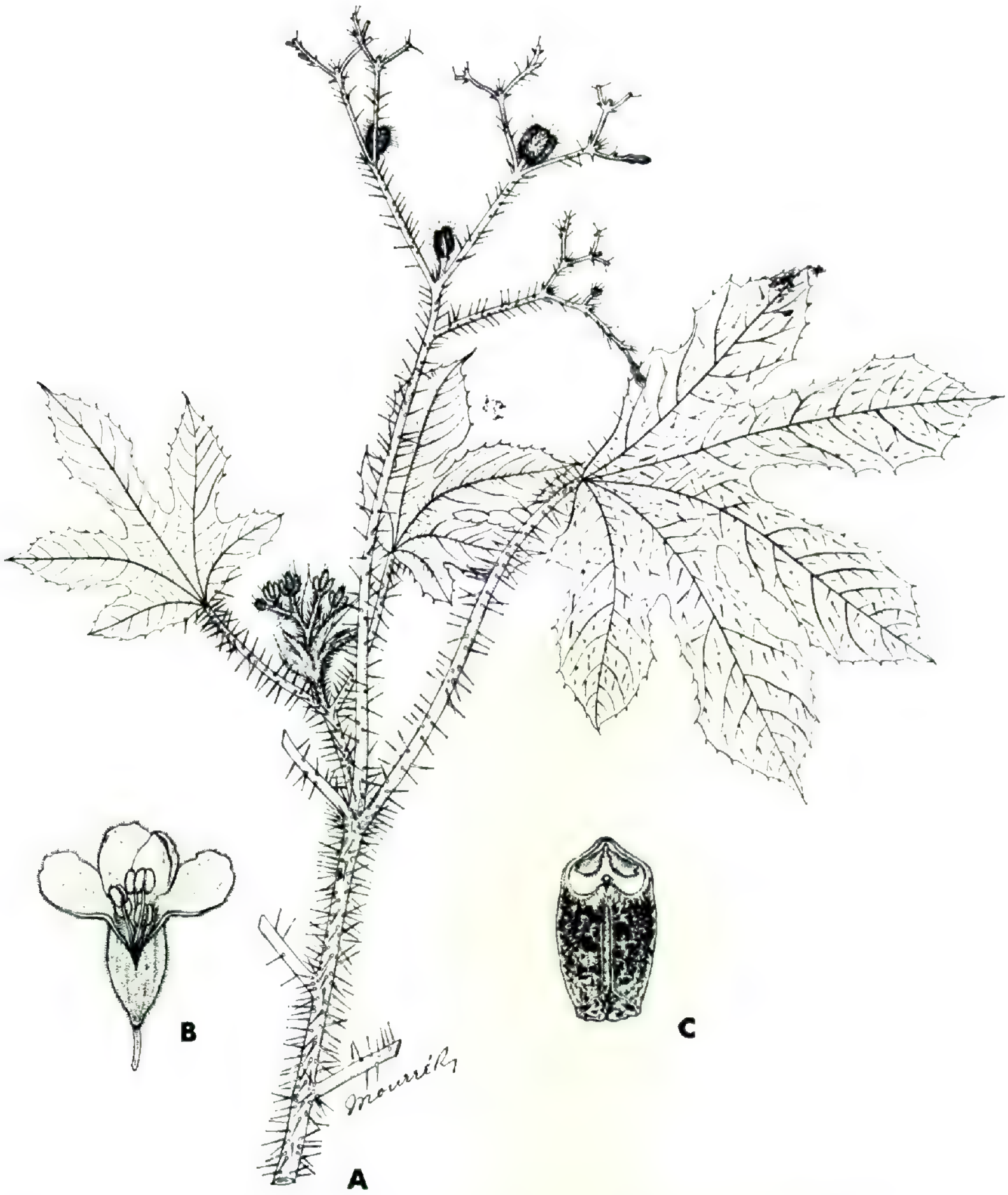

Fig. 8. *Cnidoscolus urens* (L.) Arthur: A, habit (×1/3); B, male flower, calyx split to show stamens (×2½); C, seed (×2). A, C after *Burch et al. 1357* (MO); B after *Burch et al. 1157* (MO).

glabrous, the styles nearly free, ca 1.2-1.3 mm long, incrassate, twice bifid. *Capsules* usually armed with stinging hairs, ± rugose, ca 10-12 mm long; seeds oblong-obovate, somewhat compressed, 6.5-9.7 mm long, 3.5-5.1 mm broad, pale to dark brownish or grayish, ± flecked, minutely rugulose, distinctly beaked, the caruncle deltoid, 1.2-1.5 mm high, 2-3 mm broad.

Widely distributed from eastern Mexico south to Argentina, Paraguay, and Brazil.

CANAL ZONE: Balboa, *Standley 25485* (US); Curundu, *McDaniel 5180* (MO), *Tyson 1045* (MO); Farfan Beach, *Dwyer 3065* (MO), *Tyson 1803* (MO); Gamboa, *Pittier 3712* (US); Matachin, *Kuntze 1921* (NY, US); vic of Miraflores Locks, *King 5321* (TEX), *Stern*

et al. 81 (DAV, MO). COCLÉ: banks of Río Grande, *Burch et al. 1157* (MO); wet llanos betw Aguadulce and Antón, *Woodson et al. 1226a* (A, MO, NY). DARIEN: vic of El Real, Río Tuira, *Stern et al. 454* (DAV, MO). HERRERA: Chitre to Divisa, *Burch et al. 1357* (MO). LOS SANTOS: Monagre beach, ca 5 mi SE of Los Santos, *Lewis et al. 1673* (DAV, GH, MO, US). PANAMA: Chepo, *Dodge 10728* (F, MO), *Duke 4061* (MO), *Pittier 4740* (US, type coll. of *C. adenophilus*); Las Margaritas to Río Mamoní, *Duke 5867* (MO); nr Jenine, Río Canita, *Duke 3821* (MO); 13 mi SE of La Chorrera, *King 5259* (TEX); betw Las Sabanas & Matías Hernández, *Standley 31815* (US); Panama, *Hayes 295* (NY); San José I, *Erlanson 41* (GH), *Harlow 82* (GH); *Johnston 197* (GH); Taboga I, *Macbride 2773* (F, US). VERAGUAS: hwy to Soná, 29 mi W of Santiago, *King 5279* (TEX).

The Panamanian populations of *C. urens* are not only as proteanly variable as elsewhere in much of tropical America, but appear to fall into a bimodal variation pattern in which the extremes appear as though they were distinct species. West of the Canal Zone and on the islands in the Gulf of Panama appears a form with predominantly 5-lobed leaves densely pubescent beneath, large staminate flowers with long anthers (1.1 mm or more), and relatively large seeds up to 9.3 mm long, while in the Canal Zone and to the east are found plants with smaller mostly 3-lobed glabrescent leaves and smaller staminate flowers (anthers 0.6-0.8 mm) and seeds (mostly 6.5-7 mm long). It is this small-flowered form which was described by Pax and Hoffmann as a new species, *C. adenophilus*, partly on the basis of a bracteal character which seems to be nonexistent.

Although it might appear that two species are present in Panama if one compared a few sheets of the large-flowered form (e.g. *Burch et al. 1157, Dwyer 3065, Johnston 197, Lewis et al. 1673*) with sheets of the small-flowered form (e.g. *Duke 5867, Pittier 3712, Stern et al. 81, Tyson 1045*), closer inspection will show that the readily apparent morphological differences are not sufficiently closely correlated to permit the delimitation of two different species. In other parts of Mexico and Central America a similar kind of bimodal variation pattern occurs, but there too the characters do not show any geographically distinctive correlation. The varieties recognized by Mueller and by Pax and Hoffmann appear merely to represent individually striking biotypes rather than geographic races. The cytological study by Miller and Webster (Brittonia **18:** 378, 1967) showed n = 18 in both small-flowered and large-flowered forms, although since only 3 populations were sampled, further counts would be desirable. The infraspecific variation of *C. urens* thus remains a baffling unsolved problem which evidently requires a considerably more sophisticated analysis than it has received so far.

2. **Cnidoscolus aconitifolius** (Miller) I. M. Johnston, Contr. Gray Herb. **68:** 86, 1923.

Jatropha aconitifolia Miller, Gard. Dict. ed. 8, 1768.
Cnidoscolus napeifolius (Desr.) Pohl, Pl. Brasil. Icon. Descr. **1:** 63, 1827; Kl. in Seemann, Bot. Voy. Herald 103, 1853.

Tree or arborescent shrub ca 3-8 m high; glabrous, stinging hairs sparse or absent except on petioles and leaf veins. *Leaves* thinly chartaceous; petioles ca 15-25 cm long, usually unarmed or nearly so; junction of petiole and blade with a single median dark reniform gland ca 2-3 mm wide; stipules very inconspicuous;

blades as broad as or broader than long, usually 15-25 cm across and deeply cut, with 5 main lobes and 2 smaller basal lobes, the lobes oblong to obovate, often ± runcinate-pinnatifid, sharply toothed, acuminate. *Dichasia* terminal; peduncles ca 15-30 cm long, smooth or sometimes armed, the first branches opposite, the forks of dichasium compact, the inflorescence 3-6 cm across at anthesis, the axes of inflorescence densely and closely minutely pilose. *Staminate flowers* subsessile; perianth greenish-white, minutely pilose outside but usually unarmed, ca 10-14 mm long, the perianth tube distally dilated, 6-10 mm long, lobes roundish-oblong, 4-6 mm long; disc ca 1-1.5 mm across; stamens with filaments united for most of their lengths into a column, the outer ones 4-5 mm long, the inner 8-9(-12) mm long, the anthers ca 1.5 mm long; staminodes 3, 4-5 mm long. *Pistillate flowers* subsessile or on short pedicels 1-2 mm long; calyx-segments whitish, linear-oblong, deciduous, 5-7 mm long; disc similar to that of staminate flower; ovary pubescent, the styles 3-4 mm long, connate for 1 mm at base, 3-4-fid into narrow segments. *Capsules* unarmed, green, minutely rugose, 8-12 mm long; seeds elliptic, compressed, 6-8.5 mm long, 4-5.5 mm broad, pale to dark brown and mottled, the caruncle deltoid-cordate, 1.5-2 mm high, 2-2.8 mm broad.

Native probably to eastern Mexico according to McVaugh (The Mexican species of *Jatropha*, 13, Rubber Dev. Corp., 1943); widely cultivated in Central America as a hedgerow plant. The species is extensively grown in Panama, and at least one herbarium record (*Hunter & Allen 672*) suggests that it has become naturalized.

CANAL ZONE: Government forest, Las Cruces trail, *Hunter & Allen 672* (MO). VERAGUAS: 2 mi S of Canazas, *Tyson 3708* (MO).

9. CROTON

Croton L., Sp. Pl. 1004, 1753; Gen. Pl. ed. 5, 436, 1754.

Trees, shrubs, or herbs; monoecious or dioecious; stems usually with colored sap, the indumentum (at least in part) stellate or lepidote. *Leaves* alternate; petiolate (petioles often with glands near the top); stipulate (stipules sometimes obscure or obsolete); blades pinnately or palmately veined, sometimes lobed, entire or serrate. *Inflorescences* spicate-racemose (or sometimes paniculate or subcapitate), terminal or axillary; bisexual racemes mostly with ♀ flowers solitary at proximal nodes, ♂ 1-several at distal nodes (sometimes at same nodes with ♀). *Staminate flowers* with 4-6 imbricate or (most often) valvate calyx-lobes; disc entire or dissected; petals usually 5 (rarely absent); stamens mostly 8-50, free, the filaments inflexed in bud; pollen grains globose, inaperturate, clavate; pistillode absent. *Pistillate flowers* with 4-10 (mostly 5-7) imbricate or valvate calyx-lobes; disc usually entire, rarely dissected, sometimes with staminodia; petals 5, often reduced or absent; ovary of 3 (rarely 2) carpels, the ovules 1 per locule; the styles ± free, once to repeatedly bifid or bipartite. *Fruits* capsular; seeds terete to compressed, dry, carunculate, endosperm present, the embryo with broad cotyledons.

Nearly 1000 species have been described in this natural but polymorphic genus. The majority of the species are American, but most of these occur in South

America and the West Indies; about 80 distinct species have been recognized in continental North America.

Although *Croton* is relatively poorly represented in Panama, with only 13 species, these belong to 6 different sections which include most of the important neotropical groups within the genus. A very high percentage of the Panamanian specimens of *Croton* have been misidentified in the past, partly due to the obscure treatments in the literature and partly to some necessary nomenclatural changes. None of the species proposed from Panama since the original treatments by Klotzsch and Mueller can be maintained, and it does not appear that there are any endemic Panamanian species of *Croton*, except perhaps *C. billbergianus*.

Much of the difficulty in the genus appears to be the result of a misconception by previous workers that American species of *Croton* tend to be narrowly restricted in range. The experience gained during the preparation of this treatment shows that this does not accord with the facts; several common woody Panamanian species (e.g. *C. schiedeanus*, *C. pungens* and *C. hircinus*) range far beyond our boundaries into South America. A few species, *C. panamensis* especially, are quite variable and cannot be definitively treated in a local revision such as this. Finally, it must be admitted that the species in sect. *Eluteria* pose the greatest number of problems, since these taxa are similar to various extra-Panamanian ones, and both flowers and seeds are necessary to establish specific identities. These lepidote taxa of *Croton* need careful field study in Panama and adjacent regions before the treatment proposed here can be accepted as authoritative.

a. Staminate flowers petaliferous; leaves stipulate; indumentum various.
  b. Indumentum lepidote; petals in ♀ flower reduced, similar to the ♂; leaves with deciduous stipules and eglandular petioles; inflorescences strictly axillary. (sect. *Eluteria*)
    c. Stamens 9-12, filaments glabrous; anthers 0.6-0.8 mm long; petals of ♂ flower not lepidote or with only 1 or 2 scales; seeds mostly 7 mm long or less.
      d. Leaves ± oblong-elliptic, pinnately veined; inflorescences mostly 2 cm long or more; pedicel of ♀ flower mostly 10 mm long or more ..... 1. *C. schiedeanus*
      dd. Leaves ovate, ± cordate and (3-)5-veined at base; inflorescences 1 cm long or less; pedicel of ♀ flower only 1-2 mm long .... 2. *C. pseudoniveus*
    cc. Stamens 14-17 or if fewer then filaments hirsutulous; anthers 1-1.2 mm long; petals of ♂ flower lepidote; seeds 15 mm long or more.
      e. Stamens (10-)11-13, filaments hirsutulous; leaves pinnately veined ♀ flowers mostly 3 or 4 per raceme; seeds 20-22 mm long ..... 3. *C. tenuicaudatus*
      ee. Stamens 15, filaments glabrous; leaves 3-5 veined at base; ♀ flowers mostly 1 or 2 per raceme; seeds 15-18 mm long ..... 4. *C. pyriticus*
  bb. Indumentum not lepidote, the trichomes mostly or entirely stellate or dendritic; petals in ♀ flower distinctly reduced or absent [sometimes fairly well developed in *C. panamensis*]; petioles with distinct glands at junction with blade [except in *C. hircinus*]; inflorescences terminal (at least in part).
    f. Leaves unlobed (with obscure and rudimentary indications of lobing in *C. hircinus*); ♂ calyx-lobes usually distinctly valvate in the bud; receptacle of ♂ flower usually villose; seeds not tetragonal; habit various.

g. Lower cymules of inflorescence with both ♂ and ♀ flowers at the same nodes, styles bifid or bipartite. (sect. *Cyclostigma*)

h. Pistillate flowers distinctly pedicellate (pedicels mostly 3-6 mm long; inflorescences mostly 2-4 dm long; stamens 13-20; petals of ♂ flowers with villose margins; styles glabrous or nearly so, seeds less than 5 mm long .....5. *C. panamensis*

hh. Pistillate flowers subsessile (pedicels becoming at most 2 mm long); inflorescences mostly 1-2 dm long; stamens 27-43; petals of ♂ flowers glabrous, margins minutely ciliate; styles distinctly stellate pubescent; seeds at least 5 mm long .....6. *C. pungens*

gg. Lower nodes of bisexual inflorescences with only ♀ flowers.

j. Styles twice to four times bifid; shrubs or trees (sect. *Croton*)

k. Pistillate calyx-lobes not prominently glandular-toothed; stamens 14-16; petioles with distinct apical glands.

l. Pistillate calyx-lobes elliptic to oblong, not accrescent, less than 5 mm broad; petals of ♂ flower not over 4 mm long; leaves 7-9-veined at base, entire, with petioles mostly 5-20 cm long .....7. *C. billbergianus*

ll. Pistillate calyx-lobes ovate, reduplicate-valvate, accrescent, becoming 7-8 mm long and broad; petals of ♂ flower 4.5-5 mm long; leaves mostly 5 veined at base, entire to denticulate, with petioles 1-3.5 cm long .....8. *C. fragrans*

kk. Pistillate calyx-lobes coarsely glandular-toothed below; stamens 10-12; petiolar glands obscure or obsolete .....9. *C. hircinus*

jj. Styles once bifid; annual herbs. (sect. *Geiseleria*)

m. Leaves coarsely and sharply serrate (major teeth usually not over 10 per side); stamens 8-10; styles less than 1.5 mm long, ± spreading .....10. *C. trinitatis*

mm. Leaves more finely and/or bluntly toothed; stamens 11; styles more than 1.5 mm long, ± erect.

n. Stems coarsely hispid; leaves mostly ovate, pointed at the tip, petiolar glands stalked; bracts with long gland-tipped processes; seeds 2.6-3.1 mm long .....11. *C. hirtus*

nn. Stems not coarsely hispid; leaves mostly elliptic or oblong, blunt at the tip, petiolar glands sessile; bracts eglandular; seeds 2.8-3.5 mm long .....[*C. glandulosus*]

ff. Leaf-blades deeply 3-5-lobed; ♂ calyx-lobes distinctly imbricate in bud; receptacle of ♂ flower glabrous; seeds tetragonal; annual herb. (sect. *Astraea*) .....12. *C. lobatus*

aa. Flowers apetalous; stipules and petiolar glands absent; leaves with stellate-lepidote indumentum above, lepidote beneath; stamens 10-12, filaments hirsutulous; styles 3 times bifid; seeds deciduously stellate, ca 5 mm long. (sect. *Drepadenium*) .....13. *C. punctatus*

1. **Croton schiedeanus** Schlecht., Linnaea **19:** 243, 1847.—Fig. 9(E).

C. perobtusus Lundell, Phytologia **1:** 405, 1940.

Tree ca 5-15 m high, trunk ca 1-2.5 dm thick; monoecious; indumentum lepidote. *Leaves* chartaceous; petioles lepidote, eglandular, ca 0.5-4 cm long; stipules densely lepidote, linear, capitate, (1-)2-4 mm long, caducous and thus often appearing to be absent; blades elliptic to oblong, ca 7-22 cm long, 3-9 cm broad, glabrate above, lepidote beneath with scattered scales ca 0.1-0.2 mm across (the blade appearing greenish beneath, not silvery), the venation distinctly pinnate, the major lateral veins (ca 8-12 on a side) straightish, the base obtuse to rounded, the margins entire, the apex ± abruptly contracted to a ± obtuse acumen. *Inflorescences* axillary, racemiform, ca 2-10 cm long, bisexual or male, often fascicled in the axils; ♀ flowers 1 or 2 at the base; ♂ flowers many, distal; bracts subtending solitary flowers, inconspicuous, eglandular, less than 1 mm long. *Staminate flowers* with lepidote pedicels becoming ca 2.5-3.5 mm long; calyx-lobes 5, valvate, densely lepidote, shorter than the petals; receptacle villose; petals ca 1.3-2.1 mm long, glandular-punctate, densely villose-ciliate on the margins, glabrous on the back or with 1(-2) scales; stamens (9-)10 or 11, the filaments glabrous, ca 1.5-2.5 mm long, the anthers elliptic, 0.6-0.8 mm long. *Pistillate flowers* with stiff straight lepidote pedicels becoming 10-25 mm long; calyx-lobes 5, equal, triangular or ovate, shorter than the petals; disc annular, ± adnate to the calyx; petals ca 1.8-2.1 mm long, similar to the ♂; ovary densely lepidote, scales delicately denticulate, ca 0.3-0.4 mm in diam, the styles usually 3 times bifid, ca 3-3.5 mm long, the branches slender, glabrous, spreading. *Capsules* not seen entire; cocci lepidote, verrucose, ca 8.5-12 mm long, the columella slender, 6.5-8.2 mm long; seeds compressed, brownish, smooth, obtusely beaked, 6.2-7(-9.5) mm long, 4.4-5 (-5.4) mm broad.

Widespread in lowland Mesoamerican rain forests (mostly below 500 m) from Mexico (Nayarit, Vera Cruz) south mainly along the Gulf coast to Costa Rica, Panama, Colombia, and Peru.

BOCAS DEL TORO: vic of Almirante, *Cooper 416* (GH, NY, US); Buena Vista Camp, *Cooper 591* (F, NY); Changuinola Valley, *Dunlap 497* (F, US); vic of Chiriquí Lagoon, *von Wedel 1151* (GH, MO); Cricamola, *Cooper 489* (F, US); Little Bocas, *von Wedel 2498* (GH, MO, NY), *2513* (GH, MO, NY); Water Valley, *von Wedel 1798* (GH, MO); Western River, *von Wedel 2706* (GH, MO, NY). CHIRIQUÍ: betw Hato del Jobo & Cerro Vaca, *Pittier 5421* (US); Progreso, *Cooper & Slater 165* (A, NY, US), Río Dupí, *Pittier 5219* (US); vic of San Félix, *Pittier 5288* (US). DARIEN: Tucutí, Chepigana, *Terry & Terry 1383* (F, MO).

Although this species, the most common Panamanian *Croton* with lepidote indumentum, has usually been identified as *Croton glabellus* L., it apparently is correctly designated as *C. schiedeanus* Schlecht. True *C. glabellus* (*C. nitens* Sw.), which appears to be restricted to Jamaica and the Cayman Islands, is characterized by small stipules (scarcely over 0.5 mm long), hirsutulous filaments, small seeds (4.3-6.5 mm long), and short fruiting pedicels (1.5-9 mm). In contrast, the Panamanian plants discussed here have usually larger stipules, glabrous filaments, larger seeds, and longer fruiting pedicels; furthermore, they also differ in less

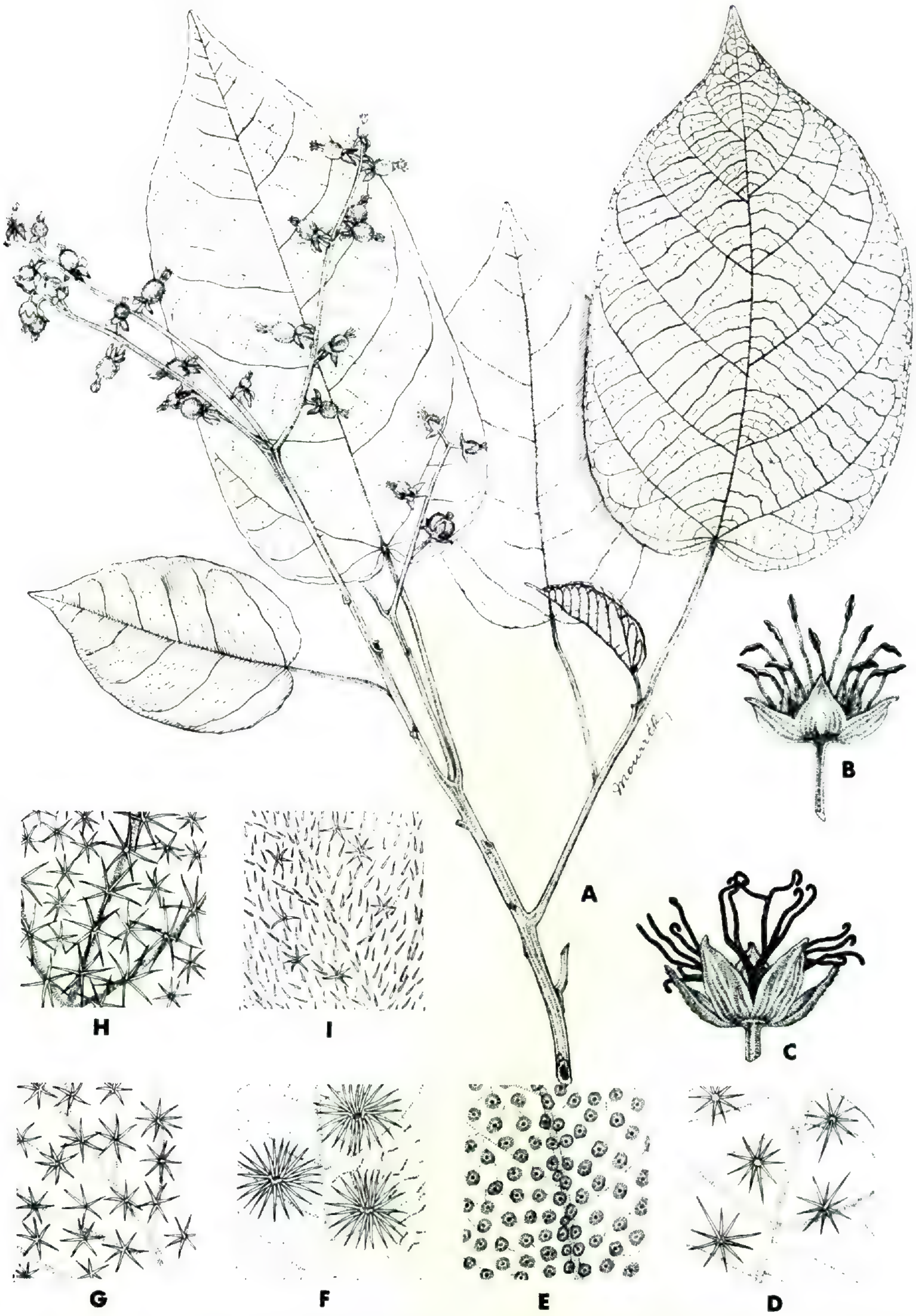

Fig. 9. *Croton billbergianus* Muell.-Arg.: A, habit (×½); B, male flower (×3); C, female flower (×3); D, indument (ca ×40). A after *von Wedel 2524* (MO); B after *Pittier 3513* (MO); C-D after *Blum & Tyson 2334* (MO). *C. schiedeanus* Schlecht.: E, indument (ca ×40). After *von Wedel 1798* (MO). *C. panamensis* (Kl.) Muell.-Arg.: F, indument (ca ×50). After *White 116* (MO). *C. trinitatis* Millsp.: G, indument (ca ×40). After *Burch et al. 1291* (MO). *C. hirtus* L'Her.: H, indument (ca ×40). After *Stern et al. 1209* (MO). *C. lobatus* L.: I, indument (ca ×40). After *Stern et al.* 346 (MO).

quantifiable characteristics such as thinner, larger leaves and more slender inflorescence axes. There can be little doubt that *C. glabellus* and *C. schiedeanus* are rather closely related, but there seems to be no reason not to treat them as distinct species.

2. **Croton pseudoniveus** Lundell, Phytologia **1:** 449, 1940.

Shrub or tree 5-6 m high; monoecious; twigs densely and smoothly lepidote. *Leaves* thinly chartaceous; petioles lepidote eglandular, mostly 10-30 mm long; stipules subulate-lanceolate, lepidote, 5-6.5 mm long; blades ovate, 6-12.5 cm long, 4-9 cm broad, green and sparsely lepidote on both sides (paler beneath), copiously and minutely glandular-punctate, 5-veined at base, with 4 or 5 additional lateral veins per side, the base narrowly cordate, the margins entire, the apex abruptly acuminate. *Inflorescences* axillary, spiciform, very compact and abbreviated (1 cm long or less), bisexual or ♂, with usually only 1 ♀ flower at base; bracts subtending solitary flowers. *Staminate flowers* with lepidote pedicels 0.9-1.5 mm long; calyx-lobes 5, valvate, triangular, lepidote, ca 1.5-1.6 mm long; receptacle villose; petals oblong to obovate, ca 2 mm long, densely villose on the margins, glandular-pustulate on the back, not lepidote; stamens 10 or 11, the filaments glabrous, 2-2.3 mm long, the anthers elliptic, pustulate on the connective, 0.6-0.7 mm long. *Pistillate flowers* with stout lepidote pedicels ca 1-2 mm long; calyx-lobes as in the ♂; disc ca 1.5 mm wide, irregularly segmented into 5 lobes, adnate to the calyx; ovary silvery-lepidote, the finely denticulate concave scales 0.7-0.8 mm wide, the styles free, spreading, ca 2.5-3 mm long, mostly 4 times bifid, the branches slender and glabrous. *Capsules* not seen; seeds (ex McVaugh, loc. cit.) 5.5 mm long.

Deciduous woodland, lowlands, western Mexico and Panama.

COCLÉ: Penonomé, roadside, *Dwyer 1999* (MO). PANAMA: 5 mi E of Canita (23 mi E of Chepo), *Tyson & Smith 4160* (MO).

The identification of these two Panamanian collections with a species heretofore recorded only from Mexico is made with some hesitation. However, the similarities in indumentum, inflorescence size, and stamen number are so impressive that the conspecificity of the Mexican and Panamanian specimens is at least a reasonable hypothesis. According to McVaugh (Brittonia **13:** 160-165, 1961), the Mexican population of *C. pseudoniveus* is distinguished by its large stiff ovarian scales up to 1 mm wide. In the Panamanian plant the scales are only 0.7-0.8 mm wide, and thus are more comparable in size to *C. reflexifolius* H.B.K.; this latter species, known from lowlands of southern Mexico, resembles *C. pseudoniveus* in leaf shape and seed size but differs in its denser foliar indumentum and androecium of 15 or 16 stamens.

In terms of geographical position, one might have expected the plant from Coclé to resemble *C. niveus* Jacquin of northern coastal Colombia. However, that species, although similar in leaf shape, has a much denser foliar indumentum (at least dorsally), and—like *C. reflexifolius*—an androecium of ca 15 stamens. It seems possible that *C. niveus* and *C. reflexifolius* may prove to be conspecific when

better material is available for study; and if the stamen number is found to be inconstant, all of these lowland populations with ovate leaves and small seeds may prove to belong to a single variable species, *C. niveus*.

3. **Croton tenuicaudatus** Lundell, Phytologia **1:** 451, 1940.

Tree 6-18 (-30?) m high; monoecious; twigs with brownish scurfily hispidulous-lepidote indumentum. *Leaves* thinly chartaceous; petioles lepidote, eglandular, (1-) 2-4.5 cm long; stipules narrowly lanceolate to subulate, densely lepidote, ca 2-4 mm long, soon deciduous; blades elliptic to elliptic-oblong, mostly 8-16 cm long, 5-8 cm broad, dark, minutely pustulate and sparsely lepidote above, paler beneath, minutely glandular-punctate, and sparsely lepidote (scales ca 0.1-0.2 mm wide); venation distinctly pinnate, the major lateral veins (ca 8-12 on a side) ± straight, the base rounded to truncate, the margins entire, ± abruptly contracted to an acuminate or caudate tip. *Inflorescences* axillary, racemiform, becoming 7-15 cm long, mostly bisexual, 1-2 per axil; ♀ flowers (1-)3 or 4 at the base; ♂ flowers many, distal; bracts subtending solitary flowers, inconspicuous, less than 1 mm long. *Staminate flowers* with lepidote pedicels 2.5-4.2 mm long; calyx-lobes 5, valvate, triangular, lepidote, ca 2.2-2.8 mm long; receptacle villose; petals elliptic to oblanceolate, 2.4-3.2 mm long, glandular-punctate, densely villose on the margins, lepidote on the back; stamens (10-)11-13, the filaments hirsutulous, 2-4.5 mm long, the anthers narrowly elliptic or oblong, 1-1.2 mm long. *Pistillate flowers* with stout lepidote pedicels 3.5-7 mm long at anthesis; calyx-lobes 5, equal, triangular or ovate, densely lepidote, 2.2-2.7 mm long; disc annular, adnate to the base of the calyx, ca 2.8 mm across; petals obovate, 2.2-2.9 mm long, similar to the ♂; ovary densely lepidote, scales minutely denticulate, ca 0.3-0.5 mm in diam, the styles usually 3 times bifid, ca 2.5-3.5 mm long, the branches slender, glabrous, spreading. *Capsules* not seen entire; cocci smooth, lepidote, ca 35 mm long, the columella winged, ca 25 mm long; seeds slightly compressed, concave-convex, reticulate-costate on sides and back, scarcely beaked, 20-22 mm long, 11-12 mm broad.

Forests at intermediate altitudes (ca 800-1000 m), Costa Rica and western Panama.

CHIRIQUÍ: betw Concepción & El Volcán, *White 309* (MO), *316* (MO). COCLÉ: N of El Valle de Antón, *Allen 3719* (MO).

The identity of this Panamanian species appears certain, as the specimens collected in Chiriquí by White are a very close match for the type collection from Costa Rica (vic of El General, *Skutch 2575* MICH). It is not certain that the fruiting collection from Coclé should be associated with the flowering specimens from further west, as the leaf shape is somewhat different and the petioles are shorter. If it does belong here, then *Croton tenuicaudatus* would appear to have the largest seeds of any species in its section.

4. **Croton pyriticus** Croizat, Jour. Arnold Arb. **26:** 186, 1945.

Tree to 20 m high; monoecious; twigs densely lepidote. *Leaves* thinly chartaceous; petioles lepidote, eglandular, 1.5-6 cm long; stipules not observed (caducous?); blades ovate, mostly 8-12 cm long, 5-9 cm broad, greenish above, sparsely lepidote, densely lepidote beneath, brownish-silvery, densely and minutely glandular-punctate on both sides; blades 3-5-veined at the broadly cuneate to truncate base, the margins entire, rather abruptly contracted into a short acumen at the apex. *Inflorescences* axillary, racemiform, 1.5-5(-10) cm long, mostly bisexual, with 1 or 2 basal ♀ flowers; bracts subtending solitary flowers. *Staminate flowers* with lepidote pedicels ca 2 mm long; calyx-lobes 5, valvate, lepidote, ca 2.5 mm long; receptacle villose; petals obovate, ca 2-3 mm long, densely villose on the margins, lepidote on the back; stamens ca 15, the filaments glabrous, the anthers 1.1-1.2 mm long. *Pistillate flowers* with pedicels becoming 10 mm long; calyx-lobes nearly as in the ♂; petals obovate, ca 2 mm long, lepidote as the ♂; ovary silvery-lepidote, the styles free, spreading, several times bifid, up to 4 mm long, glabrous. *Capsules* not seen entire; cocci lepidote, obscurely verrucose, 21-23 mm long, the columella 15 mm long; seeds somewhat compressed, smooth, carinate dorsally, obscurely and obliquely grooved ventrally, dark brownish mottled with gray, apically mucronate, 15-18 mm long, 10-11 mm broad, the caruncle 2-2.2 mm wide.

Montane forests, Costa Rica and western Panama, at 1200-1500 m.

CHIRIQUÍ: El Boquete, 4000 ft, *Davidson* 865 (A, MO).

The description of this species has been adapted partly from Croizat's original diagnosis, as the single Panamanian collection lacks flowers. The status of *Croton pyriticus* must be judged as still very uncertain. It is extremely close to *C. eluterioides* Lotsy, from Guatemala, and may prove to be only a southerly geographic race of that taxon. Croizat distinguished *C. eluterioides* by its muricate fruit with smaller seeds (11 mm long); but a collection from El Salvador (*Tucker 1229* DAV, UC) combines the muricate fruit of that species with the larger seeds of *C. pyriticus*.

There is also a striking resemblance between *C. pyriticus* and *C. niveus* Jacquin, described from the vicinity of Cartagena, Colombia. Both taxa have flowers with about 15 stamens, glabrous filaments, and similar leaves. Unfortunately fruiting specimens from the region of the type locality of *C. niveus* have not yet been collected. Since that plant furthermore appears to be a shrub growing in the lowlands rather than a tall tree in montane forests, it would appear premature to apply the name *C. niveus* to any collections available from Panama.

5. **Croton panamensis** (Kl.) Muell.-Arg. in DC., Prodr. **15**(2): 546, 1866.—Fig. 9(F).

Cyclostigma panamensis Kl. in Seemann, Bot. Voy. Herald 105, 1853.
C. denticulatum Kl., loc. cit.
Croton steyermarkianus Croizat, Jour. Arnold Arb. **21:** 86, 1940.
C. triumfettoides Croizat, loc. cit. 87.

Tree ca 5-30 m high, with trunk 0.7-6 dm thick; monoecious; young twigs ± scurfy with compact dendritic hairs. *Leaves* membranous or chartaceous; petioles scurfy 3-20 cm long, the glands at apex of petiole 2-6 (plus a cluster of smaller ones usually present on ventral side), patelliform, ± stalked, 0.5-1.2 mm across (stalk usually about equaling diam of gland); stipules linear-lanceolate to subulate, 3-10 mm long; blades mostly ovate, (7-) 10-30 cm long, (2.5-) 7-23 cm broad, sparsely pubescent above with scattered dendritic and hispid hairs (eventually glabrate), sparsely to densely tomentose beneath with stellate and dendritic hairs (these multiradiate, mostly 0.3-0.6 mm wide) and minutely glandular-dotted, 5-7-nerved at base, with ca 6-10 additional veins on either side, the veinlet reticulum prominent beneath, the base truncate to deeply cordate, the margins subentire to obscurely or rather prominently denticulate, the apex rather abruptly acuminate or caudate. *Inflorescences* terminal, usually bisexual, racemiform, (7-) 20-40 cm long, typically with the 5-20 proximal cymules ♀, the distal (and sometimes the first proximal) cymules ♂; bracts triangular or lanceolate, tomentose, inconspicuous, ca 1-1.5 mm long, subtending several flowers. *Staminate flowers* with stellate-tomentose pedicels ca 5-8 mm long; calyx-lobes 5, stellate-tomentose, triangular, 2-2.2 mm long; receptacle densely villose; petals obovate, 1.9-2.5 mm long, villose especially on the margins; stamens (13-)14-18(-20), the filaments glabrous (except at base), 2-2.8 mm long, the anthers elliptic, 0.6-0.8 mm long. *Pistillate flowers* with stout stellate-tomentose pedicels (2-)3-6 mm long; calyx-segments 5, whitish- or yellowish-tomentose outside, dark brownish inside, elliptic to oblong, ± valvate, 2.3-2.8 mm long, 1.3-1.8 mm broad; disc 2-3 mm wide, notched or lobed into 5 entire or toothed segments; petals filiform-subulate to rarely narrowly ligulate, 0.5-2.1 mm long, 0.1(-0.4) mm broad; ovary orange- or brownish-tomentose with stellate and dendritic hairs (hispid radii ca 0.3-0.6 mm long), the styles free, bifid or bipartite, glabrous or rarely sparsely stellate at the base, (2.5-)3-5 mm long, the slender branches mostly 2.5-3 mm long. *Capsules* subglobose, yellowish-brown, stellate-hispidulous, ca 6.5 mm diam, the columella slender, 3.3-3.5 mm long; seeds plump, brown, obscurely costate-roughened, 3.1-3.9 mm long, 2.6-2.8 mm broad, the caruncle ovate, ca 1 mm wide.

Lowland and montane forests, Central America (limits of distribution not clearly defined) to Colombia.

BOCAS DEL TORO: Almirante, *Cooper s.n.* (F). CANAL ZONE: Albrook, *Blum 767* (MO), *Dwyer 6715* (MO); Barro Colorado I, *Bailey & Bailey 439* (F), *White 116* (MO); Corozal, *Standley 27357* (US); Curundu, *Harvey 5190* (F); El Paraíso, *Pittier 2527* (US); Empire to Mandinga, *Piper 5526* (US); Fort Sherman, *Tyson & Ah Chu 1705* (MO); Gamboa, *Ebinger 492* (MO); betw Gamboa & Cruces, *Pittier 3773* (US); betw Gorgona & Mamei, *Pittier 2695* pro parte (GH, NY); Las Cascadas Plantation, *Standley 25811* (US), *29542* (US); Limón, *Bro. Heriberto 25* (US); vic of Madden Dam & Alhajuela, *Hunter & Allen 790* (MO); Matachin, *Kuntze 1934* (NY), *Pittier 2695* pro parte (US); Obispo, *Hayes 135* (NY). CHIRIQUÍ: Alto Lino, clearings, *Bro. Maurice 737* (US); Bajo Mona, *Davidson 480** (F, MO); id., mouth of Quebrada Chiquero, Río Caldera, *Woodson et al. 1006** (MO); Cerro Horqueta, cloud forest, *von Hagen & von Hagen 2110* (F); El Boquete, *Pittier 2927* (US); id., 1 mi SW, *Allen 4716* (MO); id., 1 mi S, *King 5318**(UC); id., Finca Collins, cloud forest, *Stern et al. 1134**(MO); id., Boquete to 3 mi N, *Lewis et al. 597* (DAV, GH, K, MO, NY, UC, US); Quebrada Velo, vic of Finca Lerida, *Allen 4678** (F, MO); Río Macho de Monte, 1 mi E of Cuesta de Piedra, *Tyson 906* (MO); vic of San Felix, *Allen 3649* (MO); Volcán Chiriquí, Potrero Muleto to summit, *Woodson & Schery*

450* (MO, US), N of Volcancito, Río Chiriquí Viejo, *Duke 9034* (MO). COCLÉ: El Valle de Antón, *Allen 2748* (A, F, US), *2482* (US). DARIEN: Caná, Río San José, *Stern et al. 634* (DAV, MO). HERRERA: 4 mi S of Los Pozos, *Tyson 2651* (MO); 10 mi S of Ocú, *Tyson et al. 2832* (MO). PANAMA: vic of Arraiján, *Woodson et al. 1375**(MO, NY); Cerro Campana, *Duke 8683* (MO); Nuevo San Francisco, *Standley 30718* (US); Sabanas, *Bro. Paul 262* (US). VERAGUAS: Río de Jesus, Río Trinidad, *Dwyer 1341* (MO).

In the conservative circumscription adopted here, *C. panamensis* includes all the Panamanian representatives of sect. *Cyclostigma* which have pedicellate flowers. The species shows considerable variation in such characters as leaf size and density of pubescence, but none of the proposed segregate taxa appear specifically distinct in our area. The most striking variant occurs in the Boquete region of Chiriquí, where plants with hispid ♂ buds and upper leaf surfaces have been designated as *C. triumfettoides* Croizat (a species described from Costa Rica); these collections have been marked by asterisks in the list of specimens. It is possible that these plants may represent a montane ecotype, as they appear to occur mostly at 1200 m and above, whereas typical *C. panamensis* is found mostly below 1200 m. Nevertheless, the plants with hispid buds are so similar in most respects to those from lower altitudes that it does not appear warranted to treat them as a distinct species.

The type locality of *C. panamensis* happens to be in this same region of Chiriquí where the deviant populations occur, but Mr. H. K. Airy Shaw has kindly examined the type specimens (at Kew) of both taxa proposed by Klotzsch and reports that neither represents the hispid variant. The second 'species' of Klotzsch, *Cyclostigma denticulatum*, is merely a trivial variation unworthy of any taxonomic recognition, as the leaf margins of *C. panamensis* vary from entire to distinctly denticulate throughout most parts of its range.

It may turn out that the present circumscription of *C. panamensis* is actually not conservative enough, for this species is in fact closely related to *C. draco* Schlecht. of Mexico and Guatemala. Typically, the more northerly species may be distinguished by its much broader foliaceous stipules; but the two taxa are much alike in other respects, and they may prove to intergrade in Honduras or Nicaragua. In that event, *C. panamensis* would have to be designated as a subspecies of *C. draco*.

6. **Croton pungens** Jacquin, Coll. **4:** 217, 1791; Icon. Pl. Rar. **3:** 19, *pl.* 622, 1794; Muell.-Arg. in DC., Prodr. **15**(2): 540, 1866.

C. standleyi Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 151, 1940.

Shrub or tree 1-5(-20?) m high; monoecious; young twigs with hispidulously stellate-tomentose indumentum. *Leaves* thinly chartaceous; petioles hispidulous-tomentose, (1-)2-6 cm long, the glands at apex of petiole 2-4, patelliform, distinctly stalked, 0.4-0.8 mm across (stalk ca 0.7-1.5 mm long); stipules linear to subulate, 1.5-4 mm long, sparsely stellate; blades ovate, ca 5-15 cm long, 2-10 cm broad, greenish above and rather sparsely pubescent with scattered oligoradiate stellate or short-stalked dendritic hairs, whitish-tomentose beneath with multiradiate dendritic hairs (ca 0.4-0.8 mm across), 5-7-nerved at base, with 3-6 additional

veins on either side, the veinlet reticulum rather prominent beneath, the base usually cordate, the margins entire to finely denticulate, the apex abruptly acuminate. *Inflorescences* terminal (sometimes pseudoaxillary), bisexual or sometimes staminate, racemiform, (3-)10-22 cm long; bisexual inflorescences with 1-15 proximal ♀ cymules, distal cymules ♂; bracts lanceolate, acute to acuminate, tomentose, ca 1-3 mm long, each subtending several flowers. *Staminate flowers* with hispidulous-tomentose pedicels 3-8 mm long; calyx-lobes 5, triangular, stellate-tomentose, 2.2-2.5 mm long, 1.1-1.5 mm broad; receptacle densely villose; petals obovate, 2.3-2.9 mm long, 1-1.3 mm broad, glabrous except for the minutely ciliate margins; stamens 27-43, the filaments 2.5-3 mm long, glabrous and ± papillose, the anthers elliptic, 0.7-1 mm long. *Pistillate flowers* subsessile, the stout pedicels even in fruit only 1-2 mm long; calyx-segments 5, ± unequal, oblong to linear-lanceolate, valvate, 2.5-3.7 mm long, 0.7-1.6 mm broad, stellate-tomentose on both faces; disc obscure; petals (staminodia?) antheriform, callose, swollen, ca 0.3-0.4 mm long; ovary closely tomentose with tawny stellate hairs, the styles free, bifid, copiously stellate-pubescent, ca 4-4.5 mm long, divided more than ½ way to the base. *Capsules* obovoid, ca 6.5-7.5 mm long, yellowish, closely stellate-scurfy, the columella slender, apically 3-pronged, ca 5.5-6 mm long; seeds plump, dull to blackish brown, rugose-costate, 5.1-5.7 mm long, 3.6-4.1 mm broad, the caruncle ovate, ca 1.5 mm wide.

Montane forests, Costa Rica to Venezuela, Peru, and Brazil; in Panama occurring above 1000 m.

CHIRIQUÍ: Finca Lérida to Peña Blanca, *Woodson & Schery 293* (MO); Paso Ancho to Monte Lirio, *Allen 1474* (A, MO); Volcán de Chiriquí, llanos, *Allen 978* (MO), *4855* (MO); id., *Davidson 892* (A, MO; type coll. of *Croton standleyi*); id., Camiseta, *Terry 1357* (MO, US).

Although at present known only from the Boquete region in extreme western Panama, this widespread species may be found on the higher summits in Darien. The type collection of *Croton standleyi* represents an unusually small-leaved form, but does not appear to show any important differences from *C. pungens*. A rather closely related species, *Croton xalapensis* H.B.K., does not occur in Panama so far as is known. It differs from *C. pungens* especially in lacking ♂ flowers at the lower ♀ nodes of the inflorescences.

7. **Croton billbergianus** Muell.-Arg., Linnaea **34:** 98, 1865; in DC., Prodr. **15**(2): 582, 1866.—Fig. 9(A-D).

Shrub or tree ca 3-10 m high; monoecious; twigs and young foliage closely scurfy with stellate hairs ca 0.1-0.2 mm across. *Leaves* membranous or thinly chartaceous; petioles stellate-scurfy, ca (2-) 5-20 cm long, the glands at apex of petiole dorsal, sessile, patelliform, yellow, thickened, ca 1-1.5 mm across; stipules subulate-lanceolate, ca 5-7 mm long, densely scurfy, soon deciduous; blades mostly ovate, ca 7-25 cm long, 5-18 cm broad, glabrate and pustulate above, minutely glandular-punctate and sparsely to densely pubescent beneath with stellate hairs, 7-9-nerved at base, with 6-10 additional veins on either side distally, the base usually cordate, the margins entire, the apex abruptly short-acuminate.

Inflorescences terminal, bisexual, racemiform or paniculate (lateral axes mostly 1 or 2), ca 3-15 cm long, often with additional smaller sometimes unisexual racemes at proximal axils; ♀ flowers 3-8 at proximal axils of most inflorescence axes, ♂ flowers many, at distal axils; bracts linear, greenish, stellate, ca 1.5-3.2 mm long, subtending solitary flowers. *Staminate flowers* with stellate pedicels ca 3-5 mm long; calyx ca 3.5-4.5 mm long, divided ca ⅔ into 5 triangular lobes; receptacle densely villose; petals elliptic to narrowly oblong, 3.5-3.8 mm long, 1-1.5 mm broad, villose, not punctate; stamens 14-16, the filaments densely villose on the proximal half, 4-5 mm long, the anthers elliptic-oblong, 1-1.4 mm long. *Pistillate flowers* with spreading or reflexed stellate-tomentose pedicels ca 3-5 mm long, becoming 7-10 mm in fruit; calyx-lobes 5, subequal, elliptic or oblong, obtuse, entire, ca 4.5-5 mm long; disc parted into 5 obcuneate, massive segments ca 1-1.2 mm wide; petals absent; ovary densely tomentose with yellowish multiradiate stellate hairs ca 0.5-1 mm across, the styles basally connate into a stout column 0.5-1 mm high, densely stellate proximally, free ends 3-4.5 mm long, 2 or 3 times bifid, the tips slender. *Capsules* spheroidal, ca 8.5-9 mm diam, stellate-tomentose, the columella slender, 4.2-4.5 mm long; seeds plump, obovate, brownish, verrucose, slightly and obtusely beaked, 4.3-5 mm long, 3.1-4.1 mm broad, the caruncle with two broad lateral lobes, 0.8-1 mm long, 1.5-2.1 mm broad.

Lowland forests; endemic to Panama, so far as is known.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Little Bocas, *von Wedel 2524* (GH, MO). CANAL ZONE: Barro Colorado I, *Aviles 100* (F), *929* (F), *952* (F), *Bailey & Bailey 100* (F), *396* (F), *Bangham 401* (A), *Dwyer 1409* (MO), *Ebinger 213* (MO), *299* (MO), *Frost 61* (F), *Kenoyer 411* (US), *Maxon et al. 6798* (US), *Salvoza 860* (A), *Shattuck 236* (A, MO), *952* (MO), *Starry 146* (F), *Standley 31436* (US), *40967* (US); Chagres, *Fendler 292* (GH, MO, US); Darien, *Standley 31611* (US); Fort Randolph, *Maxon & Harvey 6521* (US), *Standley 28718* (US); Fort Sherman, *Standley 30968* (US); Gamboa, *Pittier 3698* (US); Gatun Locks, *Dwyer 1774* (MO); Greene Memorial, *Dwyer 6759* (MO); Obispo, *Standley 31683* (US); Río Pedro Miguel, *Standley 29942* (US); vic of Río Providencia, 12 mi S Colon, *Blum & Tyson 2834* (MO). COLÓN: France Field to Catival, *Standley 30204* (US); Portobello, *Billberg 316* (photo. of type coll., DAV); vic of Sardinilla, 7-8 mi E of cement plant, *Blum & Tyson 491* (MO). DARIEN: vic of Caná, *Stern et al. 566* (DAV, MO). PANAMA: Alhajuela, Chagres Valley, *Pittier 3513* (GH, MO, NY, US); Río Mamoní, 4 mi E of Chepo, *Duke 5626* (DAV, MO).

Although commonly collected in the Canal Zone, this species appears to be of rather restricted distribution. It is similar in many respects to *C. hoffmannii* Muell.-Arg. of Costa Rica, but that plant differs in its ferruginous indumentum, looser and larger stellate hairs on the lower leaf surface, and larger smoother seeds. Much more closely related is *Croton pyramidalis* J. D. Sm., of Guatemala and Honduras, which is the northern counterpart of *C. billbergianus*. Although *C. pyramidalis* may easily be recognized by its more densely stellate and often longer-acuminate leaves, reflexed ♀ calyx-lobes, and reddish (rather than yellowish) tomentum on the ovary, it is doubtless very close to the Panamanian plant. Further studies will probably show that it should be regarded as a subspecies of *C. billbergianus*.

8. **Croton fragrans** H.B.K., Nov. Gen. Sp. Pl. **2:** 81, 1817; Muell.-Arg. in DC., Prodr. **15**(2): 556, 1866.

Shrub, sometimes arborescent, 2-10 m high; monoecious; twigs and foliage with indumentum of stellate and dendritic hairs. *Leaves* membranous or chartaceous; petioles densely stellate-tomentose, ca 1-3.5 cm long; glands at apex of petiole 2-6, patelliform, stalked, ca 0.5-0.8 mm diam (ca as broad as length of stalk); stipules elliptic or obovate, tomentose, the margins laciniate-toothed, ca 4-9 mm long; blades ovate to elliptic, ca 8-20 cm long, 4-12 cm broad, softly stellate or stellate-hispidulous (1 of the ascending radii often larger than the others) above, paler and more densely stellate (the ca 6-10-radiate hairs mostly 0.5-0.8 mm across) and minutely glandular-punctate beneath, mostly 5-(7-)nerved at base, with ca 5-8 additional veins on either side, the base obtuse or rounded to subcordate, the margins subentire or distinctly crenulate-denticulate, the apex rather abruptly short-acuminate. *Inflorescences* terminal (sometimes with additional axes in distalmost axils), bisexual or staminate, racemiform (or paniculate by aggregation), becoming ca 10-20 cm long; cymules unisexual, ♀ flowers 1-5 at proximal nodes; bracts elliptic-lanceolate, acuminate, ± laciniate-toothed, ca 2-4 mm long, subtending solitary flowers (or ♂ flowers sometimes several per bract). *Staminate flowers* with stellate-tomentose pedicels ca 6-9 mm long; calyx whitish stellate-tomentose, 4-5 mm long, divided ca ½ way or more into 5 triangular lobes; receptacle densely villose; petals obovate, ca 4.5-5 mm long, minutely glandular-punctate, densely whitish-ciliate along the margins and villose on the back; stamens 15 or 16, the filaments glandular-pustulate, glabrous, 3-3.7 mm long, the anthers elliptic-oblong, 1.2-1.3 mm long, glandular-pustulate on the connective. *Pistillate flowers* with stout tomentose pedicels 2-3 mm long; calyx-segments 5, whitish stellate-tomentose, broadly ovate, reduplicate-valvate, entire, ca 5-5.5 mm long and 4-4.5 mm broad (increasing to 7-8 mm long and broad in fruit); disc ca 2.5 mm across, cut into 5 reniform thickish segments; petals absent, replaced by tufts of stiff hairs; ovary minutely and closely pulverulent-scurfy (the trichomes ca 0.05 mm wide) and glandular-pustulate, the styles free, ca 4-5 mm long, basally thickened, distally 2-4 times bifid into slender tips. *Capsules* subglobose, closely glandular-scurfy, ca 7.5-8 mm across, the columella slender, ca 4.5 mm long; seeds plump, brownish, minutely beaked, obliquely costate on both faces, 4.3-4.5 mm long, 3.3-3.4 mm wide, the caruncle triangular, ca 1.2-1.5 mm broad.

Lowland forests, eastern Panama to northern Colombia and Venezuela.

CANAL ZONE: moist thicket, betw Fort Clayton & Corozal, old Las Cruces trail, *Standley 29066* (US); K-9 rd, *Stern et al. 977* (DAV, MO). DARIEN: Pinogana to Yaviza, *Duke 5157* (DAV, MO); Río Chico, vic of Yaviza, *Allen 5092* (MO). PANAMA: Chepo, nr river, *Tyson 1434* (MO). SAN BLAS: Ailigandí, *Dwyer 6812* (MO).

The determination of this species as *Croton fragrans* seems relatively secure, since the reduplicate-valvate accrescent ♀ calyx, glandular-pustulate floral parts, and conspicuously toothed stipules provide very distinctive features. Although some of the Panamanian collections have been confused with *C. hoffmannii*

Muell.-Arg., that Costa Rican species differs in its distinctly imbricate ♀ calyx-lobes, more ferruginous pubescence on young parts, entire stipules, and villose rather than pustulate filaments. So far no collections of *C. hoffmannii* have been seen from western Panama, where it might be expected to occur.

9. **Croton hircinus** Vent., Jard. Malm. **1:** 50, *pl. 50*, 1804.

C. populifolium Lam., Encycl. Méth. Bot. **2:** 205, 1786, non *C. populifolia* Miller (Gard. Dict. ed. 8, 1768).
C. hispidus H.B.K., Nov. Gen. Sp. Pl. **2:** 72, 1817.
Barhamia panamensis Kl. in Seemann, Bot. Voy. Herald 104, 1853.
Croton allenii Standley, Ann. Missouri Bot. Gard. **26:** 289, 1939.

Shrub or small tree 1-4 m high; monoecious; twigs rather coarsely hispid-stellate. *Leaves* thinly chartaceous, petioles rather sparsely stellate (± glabrescent), ca (0.5-)1-3(-5) cm long, the petiolar glands usually indistinct, sometimes capitate and up to 1 mm long, usually ± confounded with glandular teeth at base of blade; stipules linear to subulate, capitate-tipped and with 2 or more glandular-capitate lobes toward the base, mostly 1.5-7 mm long; blades ovate to elliptic, ca (3-)5-11 cm long, (1.5-)2-7 cm broad, sparsely stellate or stellate-hispid above with 6-10-radiate hairs, sparsely stellate (hairs ca 0.5-1.2 mm wide) and densely glandular-punctate beneath, 7 (-9) nerved at base, with ca 3-6 additional veins on either side, the base rounded to narrowly cordate, the margins distinctly and sometimes coarsely dentate or duplicidentate (teeth 15-40 on each side), the apex acute to mostly cuspidate-acuminate. *Inflorescences* terminal, bisexual, racemiform, 5-17 cm long, with 3-7 solitary ♀ flowers at proximal axils, solitary ♂ flowers at distal axils; bracts lanceolate to linear, glandular-tipped and lobed as the stipules, 2-7 mm long under the ♀ flowers and shorter under the ♂. *Staminate flowers* with stellate pedicels 1.5-4.7 mm long; calyx-lobes 5, triangular, stellate-pubescent, glandular-punctate, 2-2.8 mm long, 1.3-2 mm broad; receptacle nearly glabrous, glandular-punctate (hairs mostly on filaments and petals); petals elliptic to obovate or spathulate, 2.5-3.5 mm long, 1-2 mm broad, glandular-punctate, densely barbate-hirsute on the lower margins; stamens 10-12, the filaments densely hirsutulous in the lower third, (1.5-)2-3.5 mm long, the anthers ovate to elliptic, 0.7-1 mm long (sometimes reduced). *Pistillate flowers* subsessile, the pedicel even in fruit only 1-2 mm long, the calyx-segments 5, subequal, narrowly lanceolate to linear, coarsely glandular-toothed below, stellate-pubescent, 3.5-5 mm long, 1-3 mm broad; disc cut into 5 dark round segments ca 0.6-0.8 mm wide; petals subulate, capitate, 0.5-1.1 mm long; ovary densely stellate-tomentose, ± hispid at the apex, the styles free, ca 3-4 mm long, twice bifid (quadripartite), ± stellate-hispidulous towards the base of the slender branches. *Capsules* subglobose, copiously stellate-pubescent, becoming ca 6 mm in diam, the columella slender, ca 3.5 mm long; seeds elliptic, slightly compressed, brownish, somewhat narrowed apically but not beaked, nearly smooth (minutely striolate), 3.8-4.2 mm long, 2.9-3.1 mm broad.

Lesser Antilles, northern coastal South America, and Panama, in lowland woods below 1000 m.

COCLÉ: vic of Antón, *Woodson et al. 1711* (holotype of *C. allenii*, F; isotypes A, MO) rd to El Copé, *Burch et al. 1370* (DAV, GH, K, MO, UC, US); betw Olá and Paso del Arado, *Pittier 5025* (US); river gorge, 12 mi NE of Penonomé, *Lewis et al. 1523* (DAV, GH, MO, US). HERRERA: vic of Chitré, *Allen 1110* (GH, MO). PANAMA: betw Capira and Potrero, *Dodge & Hunter 8622* (MO); beach at Nueva Gorgona, *Duke 4517* (DAV, MO).

The Panamanian specimens of this species, to which both Klotzsch and Standley gave specific names, do not appear to differ in any essential respect from those at the other end of the range in the Lesser Antilles. The species is rather variable in pubescence, and it is conceivable that the Panamanian population might be designated as a minor subspecific variant. The name *Croton hircinus* Vent. is adopted here in place of the usually accepted *C. populifolium* Lam. because of the earlier name of Miller, based on a different plant from Jamaica.

10. **Croton trinitatis** Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. **2:** 57, 1900.—Fig. 9(G).

C. miquelensis Ferg., Annual Rep. Missouri Bot. Gard. **12:** 49, 1901.
C. tragioides Blake, Contr. U. S. Nat. Herb. **24:** 11, 1922.

Annual herb, rather sparsely branching, ca 2-8 dm high; monoecious; stems slender, sparsely to moderately appressed-pubescent with long-radiate stellate hairs (spreading hairs up to 1 mm long). *Leaves* membranous; petioles stellate-pubescent ca 0.5-3.5 cm long, the petiolar glands distinctly stalked, as long as to twice as long as broad, 0.3-0.6 × 0.2-0.5 mm; stipules greenish, ± subulate-tipped from a broader base, 0.4-1.1 mm long; blades oblong-deltoid to ovate, mostly 2-5 cm long, 1-4 cm broad, hispidulous-stellate above (hairs ca 0.2-0.8 mm across), radiate-stellate beneath (hairs ca 0.2-0.6 mm wide, 7-10-radiate), the veins at base 3(-5), with 3-5 additional veins on each side, the base obtuse, the margins coarsely serrate, major teeth ca 7-12 on a side, the apex acute. *Inflorescences* terminal or pseudoaxillary (in forks of branches), bisexual, ca 1 cm long or less, subsessile or with a short peduncle up to 0.5 cm long, with 2-4 proximal ♀ flowers and 5-8 distal ♂ flowers; bracts inconspicuous, greenish, pointed, less than 1 mm long, not or obscurely glandular at base. *Staminate flowers* with glabrous pedicels 0.3-0.6 mm long; calyx-lobes 5, with greenish sparsely hispidulous tips, ca 0.6-0.9 mm long; receptacle villose; petals ca as long as calyx-lobes, distinctly pointed; stamens 8-10, the filaments glabrous, 0.7-1 mm long, the anthers 0.25-0.3 mm long. *Pistillate flowers* with short densely pubescent pedicels which attain 1.5-2.6 mm long in fruit; calyx-lobes 5, subequal, oblanceolate or spathulate, ca 2.5-3.3 mm long, stellate-hispidulous; disc obscure; petals subulate, ca 0.3-0.4 mm long; ovary densely hispidulous, the styles bipartite, 0.7-1.1 mm long, the tips ± spreading, not inrolled. *Capsules* ca 4.5 mm long, stellate-pubescent; seeds compressed, blackish-brown, smooth (minutely foveolate-reticulate), not beaked, 3-3.6 mm long, 2.2-2.5 mm broad, the caruncle bilobed, 0.4-0.5 mm high, 1.1-1.3 mm broad.

A widespread and rather common weed in the Caribbean area (Florida and the Bahamas south to Panama, Venezuela, and Trinidad); also occurring sporadically in much of South America.

CANAL ZONE: Albrook Air Force Base, *Tyson 1100* (MO); Ancon, *Bro. Celestine 82* (US); Balboa, *Standley 25517* (US); Corozal, *Standley 27384* (US); Empire to Mandinga, *Piper 5530* (US); Fort Kobbe, *Duke 3950* (MO); Fort Randolph, *Maxon & Harvey* 6535 (US), *Standley 28688* (US); Frijoles, *Ebinger 632* (MO); Gamboa, *Standley 28487* (US); Gamboa to Cruces, *Pittier 3771* (US); Gatun Locks, *Duke 4296* (DAV, MO); Margarita Swamp, *Maxon & Valentine 7061* (US); Matachin, *Kuntze 1927* (NY); Military Rd K-9, *Ebinger 527* (MO); Miraflores, *White 117* (MO); Mount Hope Cemetery, *Standley 28808* (US); Pedro Miguel, *Bro. Heriberto 97* (NY, US); Sosa Hill, *Duke 4660* (MO); Summit, *Standley 30076* (US). COCLÉ: Aguadulce, *Pittier 4957* (US); Río Hato airstrip, *Burch et al. 1149* (MO). COLÓN: France Field to Cativa1, *Standley 30260* (US). HERRERA: betw La Avena & Pesé, *Burch et al. 1291* (MO). PANAMA: thickets nr Arraiján, *Woodson et al. 1378* (MO, NY); Camino de Las Sabanas, *Bro. Heriberto 203* (GH, US), *Standley 25859* (US); Cerro Campana, *Duke 6002* (MO); Nuevo San Francisco, *Standley 30725* (US); N of Panama city, sabanas, *Bro. Paul 525* (US); swamp E of Río Tocumen, *Standley 26562* (US); Sabana de Juan Corso, *Pittier 4496* (US); San Jose I, *Erlanson 246* (GH); Tapia River, *Maxon & Harvey 6727* (US).

This species was described by Mueller (DC., Prodr. **15**(2): 686, 1866) under the name *Croton chamaedryfolius* Grisebach; however, Grisebach's name was based on *C. chamaedryfolius* Lam., which is an *Acalypha*. Although often confused with *C. glandulosus* L., *C. trinitatis* is sharply different in its beakless seeds and fewer stamens; and it can usually be distinguished from that species by its more coarsely toothed leaves with smaller and more distinctly stalked petiolar glands.

11. **Croton hirtus** L'Her., Stirp. Nov. 17, *t. 9*, 1785.—Fig. 9(H).

C. glandulosus γ hirtus (L'Her.) Muell.-Arg. in DC., Prodr. **15**(2): 684, 1866.
C. glandulosus subsp. *hirtus* (L'Her.) Croizat., Bull. Torrey Bot. Club **75**: 401, 1948.

Annual herb becoming mostly 1-4 dm high; monoecious; stems conspicuously retrorsely stellate-hispid (hairs ca 1.5-2.5 mm long). *Leaves* membranous; petioles of leaves on main stem stellate-hispidulous, ca 3-25 mm long; stipules greenish, subulate, subentire, sparsely stellate, ca (1.5-)2.5-4.5 mm long, the glands at apex of petiole 2, distinctly stalked, 0.5-1.2 mm long, 0.1-0.3 mm broad across the flattened head; blades elliptic to more commonly ovate, 2-6.5 cm long, 1.5-5 cm broad (or smaller in depauperate specimens), bright green and rather sparsely strigose-hispid above, minutely glandular-punctate beneath, stellate with 6-10-radiate hairs (radii spreading, hairs ca 0.3-0.8 mm across), the veins at base of larger leaves 5, with ca 3-6 additional veins on each side, the base cuneate, the margins of larger leaves coarsely crenate-duplicidentate, with ca 10-15 major teeth on each side, the apex acute or obtuse. *Inflorescences* terminal, (the branching pattern of well-developed plants ± dichasial), bisexual, (0.5-)1-2.5 cm long, usually nearly sessile and subtended by reduced leaves, with mainly 5-12 proximal solitary ♀ flowers and 4-7 solitary distal ♂ flowers; bracts greenish, linear-lanceolate to subulate, glandular-capitate, with 4 or more slender-stalked ellipsoid glands at base (representing bifid stipules), 2-5 mm long (or reduced distally). *Staminate flowers* with stellate-pubescent pedicels 0.5-1 mm long; calyx-lobes 5, elliptic, hispidulous-stellate, ca 1-1.5 mm long; receptacle glabrous or nearly so; stamens 11, the filaments 0.8-1.1 mm long, glabrous, the anthers elliptic, 0.4-0.5 mm long. *Pistillate flowers* subsessile, the stout stellate-pubescent pedicels becoming 0.5-1.5 mm long in fruit; calyx-lobes usually 4 (the 5th rudimentary or obsolete), linear

to oblanceolate, distinctly unequal, the two larger 1.5-2.5 mm long and 0.4-1.1 mm broad, the two smaller 0.8-1.9 mm long and 0.2-0.3 mm broad (becoming somewhat larger in fruit); disc 5-angled, adnate to the base of the calyx-lobes; petals ellipsoidal, 0.2-0.3 mm long; ovary densely stellate-hispidulous, the styles connate at base or nearly free, ± erect, bifid or bipartite, 1.7-2.5 mm long, the style-branches slender, hispidulous, 1.5-1.8 mm long. *Capsules* subglobose, stellate-hispidulous, ca 3.5 mm diam, the columella slender, ca 2.8 mm long; seeds compressed, blackish-brown, smooth (minutely foveolate-reticulate), minutely beaked, 2.6-3.1 mm long, 1.8-2.3 mm broad, the caruncle broadly ovate, 0.4-0.6 mm long, 0.7-1.6 mm broad.

Widespread in disturbed habitats in tropical America.

CANAL ZONE: Balboa, *Macbride & Featherstone 28* (F), 35 (F, GH), *Standley 32152* (US); id., Sosa Hill, *Standley 25276* (US); Barro Colorado I, *Ebinger 245* (MO), *297* (MO); Gamboa, *Greenman & Greenman 5158* (MO); Howard Air Force Base, SE of Kobbe Beach, *Oliver & MacBryde 1878* (DAV, GH, MO); Miraflores Bridge, *Dwyer 1004* (MO); Miraflores Locks, *Stern et al. 76* (DAV, MO); Sosa Hill, *Duke 4660* (DAV, MO); CHIRIQUÍ: vic of Boquete, llanos Francia, *Stern et al. 1209* (DAV, MO); Tole, *Tyson et al. 4217* (MO). COCLÉ: betw Las Margaritas and El Valle, *Woodson et al. 1270* (A, MO, NY). COLÓN (?): betw France Field and Cativa1, *Standley 30419* (US). PANAMA: vic of Chepo, Camino del Boticario, *Pittier 4691* (US); Juan Franco, *Bro. Heriberto 270* (US); sabanas N of Panama City, *Bro. Paul 543* (US); San José I, East Harbor, *Erlanson 246* (NY, US); id., Main Camp, *Johnston 999* (GH).

Most of the reports of *Croton glandulosus* L. from Panama represent the present species (a smaller proportion prove to be *C. trinitatis*). No authentic Panamanian specimen of *C. glandulosus* has been seen, so that the species cannot be accepted as a member of the flora, although it may possibly be introduced in the future.

Despite the prevailing tendency of botanists to treat *C. hirtus* as a synonym of *C. glandulosus* (mainly due, one suspects, to the influence of Mueller's treatment), the two taxa are actually quite distinct. *Croton glandulosus* diverges sharply from *C. hirtus* in lacking the conspicuous hispid pubescence on the stems, and further differs in its sessile petiolar glands, less conpicuously toothed leaf-blades, and glandless floral bracts.

12. **Croton lobatus** L., Sp. Pl. 1005, 1753.—Fig. 9(I).

Astraea seemannii Kl. in Seemann, Bot. Voy. Herald 103, 1853.
Croton lobatus ζ *seemannii* (Kl.) Muell.-Arg. in D.C., Prodr. **15**(2): 669, 1866.

Annual herb becoming mostly 5-10 dm high; monoecious; stems sparsely stellate, soon glabrate. *Leaves* membranous, petioles stellate-pubescent, glabrescent, (2-)4-8 cm long, the glands at apex of petiole several on the ventral side, globular, minute (ca 0.1-0.15 mm wide); stipules lanceolate to setaceous, acute or acuminate, subentire, ca 0.7-2.5 mm long; blades deeply lobed into 3(-5) elliptic-lanceolate to obovate-lanceolate acuminate lobes, ca 3-7 cm long, 5-9 cm broad, hispidulous-strigose on both sides with a few scattered stellate hairs beneath, obscurely glandular-punctate; blades 3-5-nerved at base, lobes with ca 5-8 veins on each side, the base truncate to broadly cordate, the margins rather coarsely serrate or crenate,

central lobe with ca 5-20 teeth on each side. *Inflorescences* terminal but sometimes appearing axillary, bisexual, racemiform, mostly 7-15 cm long, with (1-)3-7 solitary ♀ flowers at proximal axils, cymules of 2-4 ♂ flowers at the 5-12 distal axils; bracts lanceolate, greenish, somewhat pubescent, often with basal lobes, ca 1-2.5 mm long under the ♀ flowers, somewhat smaller under the ♂. *Staminate flowers* with glabrous pedicels ca 1.5-2.5 mm long; calyx-lobes 5, distinctly imbricate, elliptic, rounded at the tip, glabrous or very sparsely hispid, 1-1.2 mm long, 0.8-1 mm broad; receptacle glabrous; petals elliptic, glabrous, not punctate, 1.2-1.5 mm long, 0.5-1 mm broad; stamens (8-)12-15, the filaments glabrous, 0.9-1 mm long, the anthers broader than long, ca 0.3 × 0.4-0.5 mm. *Pistillate flowers* subsessile, the stellate pedicel becoming ca 2-3 mm long in fruit; calyx-segments 5, valvate, subequal or somewhat unequal, oblanceolate to linear, acute, greenish, sparsely hispidulous, ca 4.5-5.5 mm long, 1-1.5 mm broad, toothed with stalked glands in the lower half; disc dissected into 5 reniform segments ca 0.3-0.4 mm wide; ovary sparsely to densely pubescent with stellate and/or simple hairs, the styles essentially free, spreading, strigose-hipidulous, quadrifid in the distal half, glabrous or stellate-hispidulous, 2.5-3.5 mm long, the slender subulate branches 0.7-2.2 mm long. *Capsules* subglobose, 3-lobed, sparsely stellate, ca 6-6.5 mm in diam, the columella slender, ca 4 mm long; seeds oblong, tetragonal, brownish or fuscous, apically beaked, prominently rugulose-costate, 4.1-4.4 mm long, 2.2-3 mm broad, the caruncle reniform-peltate, 1-1.2 mm long and 1.9-2.2 mm broad when fully expanded (but often shrunken to smaller dimensions).

Common in weedy habitats, southern Florida and the Bahamas south to Peru and Brazil.

CANAL ZONE: vic of Río Cocoli, Rd K-9, *Stern et al.* 346 (DAV, MO). PANAMA: Río Abajo, *Bro. Heriberto* 284 (GH, NY, US).

The Panamanian population of this widespread weed was referred to var. *seemannii* by Mueller, but that variety appears to be synonymous with var. *lobatus*, since Linnaeus founded his species on a similar plant from Vera Cruz, Mexico. The Central American and West Indian populations of this species may prove to comprise a single geographic race characterized by glabrous to sparsely pubescent ovary and predominantly simple hairs on the upper leaf surface.

13. **Croton punctatus** Jacquin, Coll. **1:** 166, 1787; Icon. Pl. Rar. **3:** 19, *t. 621*, 1789.

C. maritimus Walter, Fl. Carol. 239, 1788.

Shrub with spreading, flexible ± succulent branches, less than 1 m high; monoecious; twigs with dense indumentum of lepidote (but deeply lobed) scales. *Leaves* thickish; stoutish lepidote petioles 7-20 mm long, the petiolar glands and stipules absent; blades flexible-leathery, elliptic to more commonly ovate, ca 2-4 cm long, 1.2-3 cm broad, greenish and closely stellate-lepidote above (the scales ca 0.3-0.5 mm wide, with the 10-15 radii barely fused at base), pale and silvery-lepidote beneath (the densely overlapping scales ca 0.6-0.7 mm wide with ca 15-20

radii united ¼ to ⅓ their length); blades 3-5-nerved at base, the other veins completely indistinct, the base rounded to subcordate, the margins entire, the apex acute. *Inflorescences* terminal, bisexual (reduced ones sometimes unisexual), distinctly pedunculate, ca 1-2 cm long, with 1 (rarely 2) basal ♀ flower and a pedunculate terminal capitulum of ca 4-6 ♂ flowers; bracts stellate-lepidote, caducous and inconspicuous, not over ca 1 mm long. *Staminate flowers* subsessile or with short stout pedicels less than 1 mm long; calyx-lobes 5, imbricate, ovate to elliptic, obtuse, lepidote on the back, villose on the margins, ca 2.5 mm long and 1.2-1.6 mm broad; receptacle pilose; petals absent; stamens 10-12, the filaments hirsutulous, up to 1.5 mm long, the anthers elliptic, 0.8-0.9 mm long, the connectives pustulate. *Pistillate flowers* subsessile, the stout pedicel only ca 1 mm long in fruit (fruits superficially appearing pedunculate when at the end of the inflorescence peduncle); calyx-lobes 5, subequal, imbricate, ovate to triangular, lepidote, entire, becoming 3-3.5 mm long, 1.8-2.3 mm broad; disc annular, adnate to the base of the calyx, 2.8-3.2 mm wide; petals absent; ovary densely lepidote (scales with ca 12-20 radii connate less than ⅓ their lengths, ca 0.5-0.9 mm wide), the styles free, spreading, 3 times bifid, stellate-lepidote below, ca 1.5-2 mm long. *Capsules* subglobose, 3-lobed, stellate-lepidote, ca 7-8 mm broad, the columella apically dilated-alate, ca 4-4.5 mm long; seeds plump, ovoidal, grayish or silvery with brownish spots or mottling, sparsely and deciduously stellate, 4.9-5.1 mm long, 3.9-4.2 mm broad, the caruncle massive, convex, subentire, ca 2.5 mm wide.

Deep sand on marine beaches, North Carolina south to Panama, with outliers in Bermuda and Cuba.

BOCAS DEL TORO: beach at Bar Mouth, Changuinola Valley, *Dunlap 521* (F). CANAL ZONE: beach, vic of Fort Sherman, *Standley 31196* (US). COLÓN: Colón, *Riley 103* (US); beach nr Viento Frio, *Pittier 4112* (US).

The distribution of this distinctive species is rather curious, since it forms a nearly continuous population (where substrates permit) along the entire Atlantic and Gulf coasts of the North American mainland, but offshore has invaded only Bermuda and western Cuba, being absent from areas such as the Bahamas where it might well be expected. The Panamanian plants, which represent the southernmost extension of the species and the section to which it belongs, appear very similar in all respects to those in North Carolina, at the opposite end of the range.

10. CAPERONIA

Caperonia St.-Hil., Hist. Pl. Remarq. Brésil 244, 1824.

Ditaxis sect. *Caperonia* (St.-Hil.) Baillon, Adansonia **4**: 272, 1865.

Herbs, annual or perennial, sometimes rhizomatous or suffruticose; monoecious (in Panamanian species). *Leaves* alternate, petiolate, stipulate; blade pinnately or palmately veined, margin serrate. *Inflorescences* axillary, usually bisexual, racemiform or spiciform, with 1-5 basal pistillate and several distal staminate flowers; bracts subtending solitary flowers. *Staminate flowers* with pedicels articulate; calyx usually 5-lobed, valvate in the bud; petals 5, often unequal, basally

adnate to the staminal column; disc absent; stamens 10, in 2 superposed whorls of 5, the anthers dehiscing longitudinally; pollen grains ± oblate-spheroidal, reticulate, 6-colporate (in Panamanian species), germ pores large; pistillode present. *Pistillate flowers* sessile or sometimes short-pedicellate; calyx-lobes typically 5, with 0-5 smaller supernumerary lobes; disc obsolete; ovary of 3 carpels, muricate and sometimes hispidulous as well, the ovules 1 per locule, the styles 3, ± deeply 3-7-lobed. *Fruits* capsular, verruculose; seeds spheroidal, ecarunculate, minutely foveolate, with narrow raphe, the endosperm copious, the cotyledons broader than radicle.

A predominantly American genus of 35-40 species, related to *Argythamnia* but separable by its glandular pubescence, leaf venation, pistillode-bearing staminate flowers, pollen grains, seed ornamentation, and chromosome number.

The taxa of *Caperonia* in Panama show the rather bewildering kind of variation they display elsewhere, and no less than 6 species have been proposed on the basis of Panamanian specimens. It is possible that some of the apparent variability is due to hybridization between *C. paludosa* and *C. palustris*, but there is really no convincing evidence for this. All of our taxa belong to sect. *Caperonia;* plants of sect. *Aculeolata* Pax & Hoffmann are strictly South American. *Caperonia castaneifolia* (L.) St.-Hil. has not been encountered in Panama; the records of it by Klotzsch (in Seemann, Bot. Voy. Herald 103, 1853) and Hemsley (Biol. Centr.-Amer. Bot. **3:** 120, 1883) appear to have been founded on misdetermined specimens of *C. palustris*. Nevertheless, since it is very widespread in tropical America, it may eventually be detected in Panama. It may be distinguished by its complete lack of gland-tipped setae, ovate stipules, and subequal petals (the staminate exserted considerably beyond the calyx).

a. Pistillate flowers distinctly pedicellate (pedicel in fruit over 2 mm long); ovary hispidulous as well as muricate; styles 3-lobed; pistillode in ♂ flowers entire; leaves closely and shallowly toothed ..... 1. *C. neglecta*

aa. Pistillate flowers sessile or nearly so (pedicel in fruit less than 1 mm long); styles mostly 5-7-lobed; pistillode in ♂ flower apically lobed; leaves more sharply and remotely toothed.

b. Ovary muricate but not hispidulous; stipules lanceolate (mostly 2.5-5 times as long as broad); pistillate petals subequal, shorter than the calyx; stems and ♀ calyx with gland-tipped setae; leaves ovate to linear-lanceolate. ..... 2. *C. palustris*

bb. Ovary hispidulous as well as muricate; stipules more or less ovate (mostly 1-2.5 times as long as broad); pistillate petals equaling or exceeding the calyx; stems with appressed non-glandular hairs only, the calyx with a few marginal gland-tipped setae; leaves narrowly lanceolate to linear. ..... 3. *C. paludosa*

1. **Caperonia neglecta** Webster, Ann. Missouri Bot. Gard. **54:** 192, 1967.

Annual herb with distinct taproot, ca 2-5 dm high; stems moderately to copiously branched, angled, striate, densely shaggy-hirsute with gland-tipped hairs and hispidulous-strigose with appressed sharp-pointed hairs. *Leaves* membranous; petioles pubescent ca 1.5-5.5 mm long; stipules lanceolate, ciliate with sharp-pointed hairs, ca 1.5-4.5 mm long, 0.4-0.9 mm broad; blades mostly elliptic, mostly 3-7 cm long and 1-3 cm broad, pubescent on both sides with both gland-

ular and pointed hairs, the veins and midrib raised on both sides, the secondary veins parallel and at right angles to primary ones (venation thus ± scalariform), the base obtuse or rounded, the margins shallowly serrate with mostly 15-30 teeth, the apex evenly narrowed or tapering to an acute point. *Racemes* 1.5-3 cm long, with 1-3 basal ♀ and several distal ♂ flowers; rachis pubescent as the stem; bracts with sharp hairs at the apex and on the margins. *Staminate flowers* with short hispidulous pedicels; calyx-lobes unequal (3 of them smaller and less deeply cut), sparingly hispidulous, 1-veined, acute or apiculate; petals obovate, distinctly unequal, the 3 larger ones ca 1.5-1.8 mm long and 0.6-0.8 mm broad, the two smaller ones ca 1.1-1.3 mm long and 0.5-0.6 mm broad; upper stamens with filaments about as long as or longer than the anthers, the lower stamens with filaments shorter than anthers, the anthers 0.3-0.4 mm long; pistillode entire, rounded, ca 0.25-0.3 mm long. *Pistillate flowers* with hispidulous pedicels becoming 2.4-2.7 mm long in fruit; calyx-lobes 5, subequal, convexly rounded on the back, tipped with a sharp seta, margins with gland-tipped and with sharp hairs, in fruit ca 1.5-2.2 mm long and distinctly longitudinally ribbed; petals subequal, narrowly elliptic, 1.2-1.6 mm long, 0.3-0.5 mm broad, exserted beyond the calyx-lobes; ovary densely hispidulous proximally, muricate distally, the styles ca 1 mm long, deeply 3-lobed, the lobes rather slender. *Capsules* 4.5-5.5 mm broad, greenish with reddish verrucae, the columella ca 1.5 mm long; seeds spheroidal, fuscous-brown, 2.3-2.7 mm in diam.

Known only from a few weedy localities in Panama.

CANAL ZONE: Corozal, brushy slope, *Standley 27376* (US), *27386* (US). PANAMA: Camino del Boticario, near Chepo, *Pittier 4545* (holotype US); Tumba Muerto Rd, nr Panama, grassy field, *Standley 29769* (US); id., moist woods, *Standley 29815* (US).

Pittier collected the type specimen of this species at the same locality with *C. palustris* and *C. paludosa;* but his specimen was annotated by Kathe Hoffman as *C. palustris;* Standley labeled his collections the same. Due to its copious glandular pubescence and many-toothed blades, *C. neglecta* does superficially resemble *C. palustris,* but is easily separated by its hispidulous ovary and unequal male petals. In many ways, *C. neglecta* is intermediate between the other two Panamanian species, having leaves and glandular hairs similiar to those of *C. palustris* but the petals and hispidulous ovary of *C. paludosa.* This, and the sporadic occurrence of *C. neglecta* sometimes in association with the other 2 species, suggests the possibility of its being a hybrid between them. Against this, however, must be set the fact that *C. neglecta* has some unique characters not represented in either of its two Panamanian congeners, especially its pedicellate pistillate flowers and unlobed pistillode. Furthermore, it appears to produce viable pollen and seeds. There seems to be no sufficient reason, therefore, not to recognize it as a distinct species; but these questions certainly indicate the desirability of a thorough field study of the *Caperonia* populations in the savannas of western Panama province.

2. **Caperonia palustris** (L.) St.Hil., Hist. Pl. Remarq. Brésil 245, 1824.

Croton palustris L., Sp. Pl. 1004, 1753.

Herb, usually annual, taprooted and also often rooting at the lower nodes; stems erect, subterete, striate, sometimes fistulose, usually not with prominent aerenchyma at base, ca 3-10 dm high, hirsute with gland-tipped hairs intermixed with appressed, relatively inconspicuous, sharp-pointed hairs. *Leaves* membranous; petioles 1.5-2.5 mm long, usually hispidulous and prominently pubescent with glandular hairs; stipules lanceolate, 2-4.5 mm long, 0.5-1.1 mm broad, often marginally ciliate with glandular and/or non-glandular hairs; blades variable in shape (ovate or elliptic to lanceolate or even linear lanceolate), mostly 4-10(-12) cm long, 0.5-5 cm broad, sparsely pubescent (with both glandular and non-glandular hairs) to glabrate on both sides, the midrib and veins (ca 6-15 on a side) prominent, the primary veins straight, the secondaries tenuous, perpendicular to primaries (venation thus ± scalariform), the base obtuse or rounded to subcordate, the margins rather sharply serrate and minutely scabrous, with ca (10-) 15-35 teeth on a side, the apex broadly rounded to more often distinctly narrowed or pointed. *Racemes* spiciform, mostly 4-7 cm long, with (1-)2 or 3(-5) basal ♀ and several distal ♂ flowers; rachis hispidulous throughout, usually with glandular setae at least on the peduncle; bracts acute, persistent, glabrous. *Staminate flowers* with short glabrous pedicels; calyx glabrous, acutely lobed; petals 5, subequal, obovate, ca 1.5 mm long; stamens 10, the upper filaments as long as or longer than anthers, the lower filaments nearly contiguous to upper ones, shorter than the anthers, the anthers ca 0.5 mm long; pistillode apically 2-4-lobed, 0.6-0.8 mm high. *Pistillate flowers* subsessile, the very short glabrous pedicels less than 1 mm long even in fruit; calyx-lobes 5-9, usually unequal (with 4-6 larger inner lobes and 1-4 smaller outer ones), flattish, thin, not ribbed, acute, ordinarily copiously glandular-hirsute on margins and back, the longer ones ca 3.5-5 mm long in fruit; petals subequal, narrowly elliptic, pointed, (0.8-)1.3-1.9 mm long, 0.3-0.7 mm broad, not exserted beyond the calyx-lobes, ± deciduous; ovary glabrous proximally, densely glandular-muricate distally, the styles 1.1-1.7 mm long, usually deeply 5-7-lobed, the lobes slender. *Capsules* 5.1-5.7 mm in diam, stramineous-green with dark green verrucae; seeds spheroidal, fuscous, 2.4-2.7 mm in diam.

A widespread neotropical weed, usually of ditches, swamps, and other wet habitats, occurring from Florida and Louisiana south to Argentina and Uruguay.

CANAL ZONE: Balboa, *Standley 26108* (US); Chiva-Chiva trail nr Miraflores Lake, *Tyson 1383* (MO); Coco Solo, *Elias & Kirkbride 1623* (GH, MO, US); Empire, *Pittier 3728* (GH, US); Fort Kobbe, *Duke 3959* (DAV, MO); France Field to Cativa1, *Standley 30256* (US); Gamboa, *Standley 28466* (US); Gatun, *Duke 4303* (DAV, MO), *Piper 5998* (US); Gorgas Lab, *White 145* (F, MO); vic of Summit, *Standley 26965* (US), *Tyson & Blum 1993* (MO). COLÓN: vic of Sardinilla, 7-8 mi E of cement plant, *Blum & Tyson 482* (MO). DARIEN: vic of El Real, *Duke 4854* (MO) *Stern et al. 617* (MO). LOS SANTOS: 3 mi S of Carreta, *Burch et al. 1252* (MO). PANAMA: Camino de Las Sabanas, *Bro. Heriberto 202* (GH, US); 5-6 mi E of Chepo, *Duke 4034* (MO), *4035* (DAV, MO), *Pittier 4546* (US); vic of El Llano, *Duke 5500* (MO); Pacora, *Woodson et al. 734* (F, MO); Panama, Juan Franco Racetrack, *Standley 27683* (US); Río Tatare, *Woodson & Schery 999* (MO); San José I, *Johnston 1042* (GH); Tocumen, *Dwyer 1852* (MO). PROVINCE UNKNOWN: s. loc., *Hayes 703* (K).

In Panama, this aggressive and highly variable weed has been found in gardens, fields, roadsides, and swamps, often occurring together with *C. paludosa*. Some of the extremely narrowly-leaved variants of *C. palustris* suggest possible hybridization with *C. paludosa*, but other characters do not provide any convincing support for such a hypothesis.

Prain (in Fl. Trop. Afr. **6**(1): 831, 1912) reported *C. latifolia* Pax from Panama on the basis of *Hayes 703*. However, examination of this specimen at Kew shows it is clearly a plant of *C. palustris*.

3. **Caperonia paludosa** Kl., London Jour. Bot. **2:** 51, 1843.—Fig. 10.

C. panamensis Kl. in Seemann, Bot. Voy. Herald 103, 1853.
C. panamensis Pax & Hoffm., Pflanzenreich **63** (IV, 147, VII): 424, 1914.
C. angusta Blake, Jour. Wash. Acad. Sci. **14:** 288, 1924.
C. stenomeres Blake, loc. cit.

Herb to 6 dm high, sometimes woody at the base; stems subterete, striate, often hollow-fistulose, sparingly hispidulous-strigose when young, soon glabrate, branches weak and often straggling. *Leaves* membranous or chartaceous; petioles usually hispidulous, 1-7 mm long; stipules ovate or triangular, 0.8-2.5 mm long, 0.5-1.1 mm broad (ca 1-2 times as long as broad), entire or marginally and apically hispidulous, not becoming reflexed; blades narrowly lanceolate to linear, ca 4-12 cm long, 2-7 mm broad, glabrous except for a few appressed hairs on midrib and veins, the primary veins ca 6-15 on a side, the secondaries ± perpendicular but often inconspicuously or invisible, the base narrow or rounded, the margins remotely and inconspicuously to sharply serrate, with ca 6-20 teeth on a side (sometimes subentire), the apex acute to acuminate. *Racemes* spiciform, 1.5-3 cm long, with 1 or (less commonly) 2 basal ♀ flowers; rachis appressed-hispidulous; bracts acute, entire or marginally hispidulous. *Staminate flowers* with short glabrous or hispidulous pedicels; calyx-lobes subequal, ca 1.4-1.5 mm long, acute, glabrous; petals obovate, subequal, or sometimes unequal, 1.2-2.2 mm long, 0.5-1 mm broad, the upper filaments longer than anthers, the lower shorter to slightly longer than the anthers, the anthers 0.4-0.5 mm long; pistillode cylindric, shallowly 3-lobed (sometimes barely emarginate), 0.4-0.9 mm long. *Pistillate flowers* subsessile, the glabrous pedicels less than 1 mm long in fruit; calyx-lobes 5 or 6 with 0-3 smaller outer lobes (or sometimes calyx of 3 large inner and 3 small outer lobes), flattish, thin, not ribbed, acute, sparsely glandular-setulose on the margins, to ca 2.5 mm long in fruit; petals subequal, equaling or exceeding the calyx-lobes at anthesis, 1.2-3 mm long, 0.6-1 mm broad; ovary strigose proximally, densely glandular-muricate distally, the styles ca 1.5 mm long or less, 4-5-lobed ½ to ⅔ their length, the lobes rather thick and fleshy. *Capsules* 4.8-5.1 mm in diam, strigose and muricate; seeds spheroidal, ca 2.4 mm long.

Marshes, swamps, and savannas, eastern Mexico to the Guianas.

CANAL ZONE: betw Fort Clayton & Corozal, *Standley 29093* (US). COCLÉ: Aguadulce, *Pittier 4922* (US); Las Margaritas to El Valle, *Woodson et al. 1750* (F, GH, MO); Penonomé, *Williams 212* (NY). PANAMA: Camino del Boticario, Chepo, *Pittier 4547* (iso-

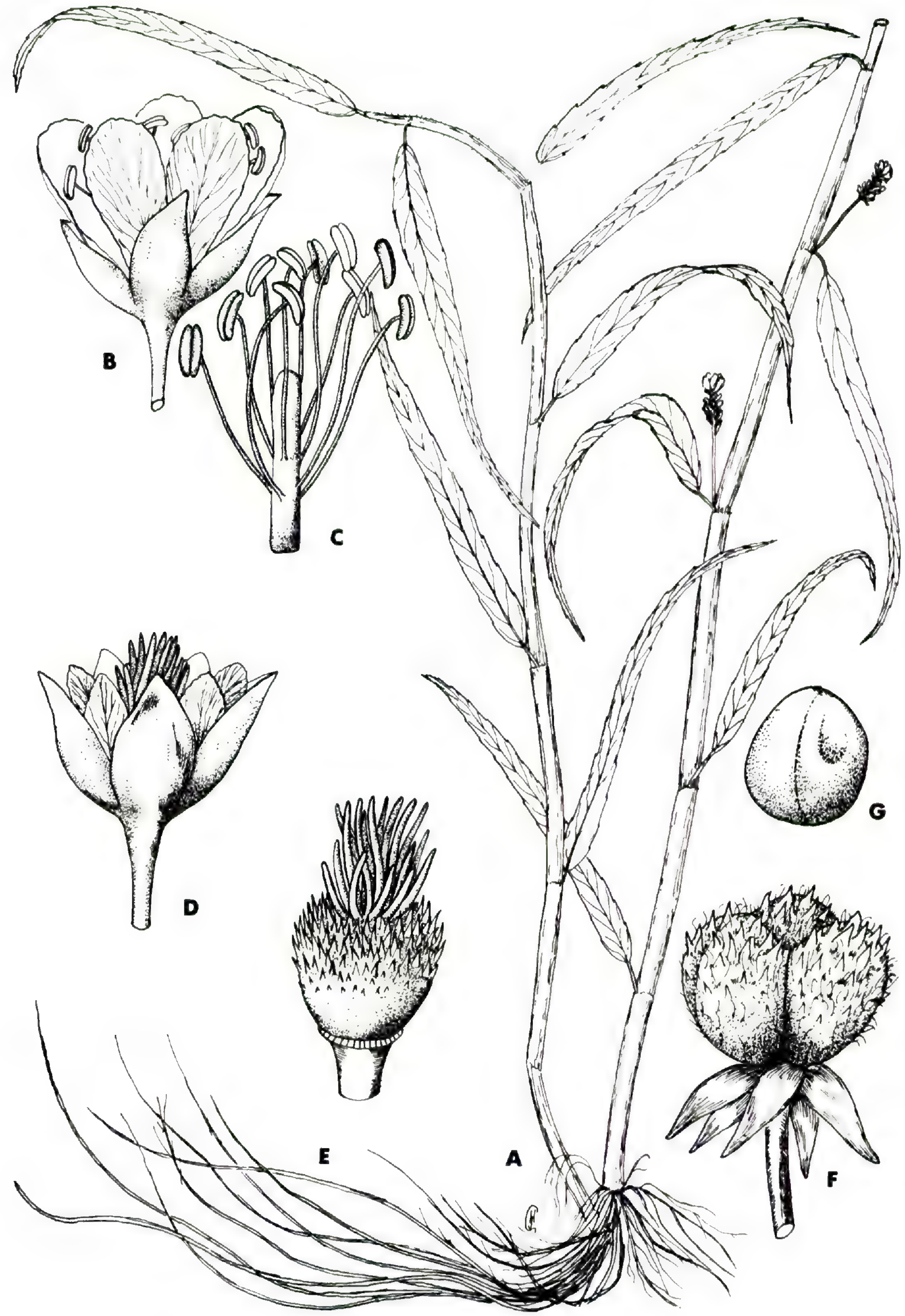

Fig. 10. *Caperonia paludosa* Kl.: A, habit (×½); B, male flower (×10); C, stamens (×20); D, female flower (×12); E, ovary (×15); F, fruit (×6); G, seed (×8). A-E after *Woodson et al.* 735 (MO); F-G after *Dodge et al. 16912* (MO).

type of *C. panamensis* Pax & Hoffm., US); La Joya, nr pond, *Dodge et al. 16912* (MO); Juan Díaz, *Standley 26224* (US); Las Sabanas, *Bro. Heriberto 295* (NY, US), *Killip 3121* pro parte (US); Matías Hernández, *Pittier 6927* (holotype of *C. angusta,* US), *Standley 28910* (US), *31987* (US); Nuevo San Francisco, *Standley 30765* (US): wet savannas E of Pacora, *Woodson et al. 735* (A, F, MO, NY); ditches & wet savannas nr Panamá, *Hayes 714* (K, NY); swamps nr Panamá, *Seemann 119* (type coll. of *C. panamensis* Kl., K, BM); Río Tapia, Juan Díaz, Killip *3121* pro parte (NY); Río Tocumen, *Standley 26571* (US).

The variable Panamanian populations of this species have been confusingly treated in the literature, and the synonymy has become excessively involved. However, despite the application of 4 names (2 of these fortuitously identical), only a single narrow-leaved species seems present in Panama, and it does not appear to be specifically different from the widespread *C. paludosa.* Mueller (in DC., Prodr. **15**(2):755, 1866) and Pax [Pfanzenreich **57** (IV, 147, VI): 35, 1912] may have partially initiated the confusion by describing the pistillate flowers of *C. paludosa* as having rudimentary petals. In fact, however, examination of the type collection of *C. paludosa* (*Schomburgk 109,* K) shows that the pistillate flowers have petals ca 1.5-2 mm long, and are also well developed in the type collection of *C. panamensis* Kl. (*Seemann 119,* K). The petals are early deciduous in *C. paludosa,* which may account for these mistakes of description, and for the curious error made by Pax and Hoffmann in redescribing Klotzsch's species under the same specific epithet.

Blake compounded all the confusion by uselessly renaming *C. panamensis* Pax & Hoffmann as *C. stenomeres,* and by proposing an additional species of *C. angusta* on the basis of a variant specimen (*Pittier 6927,* US) with 7-8-lobed pistillate calyx and a distinctly trilobed pistillode. Most of the Panamanian collections, however, resemble the type of *C. panamensis* Pax & Hoffmann in having the pistillate calyx 5- or 6-lobed. In any event, the plants with 7 or 8 pistillate calyx-lobes do not seem to be specifically distinct; whether the large number might be due to crossing with *C. palustris* must be tested by field observations.

11. ARGYTHAMNIA

Argythamnia P. Browne, Civ. Nat. Hist. Jam. 338, 1756.

Ditaxis Vahl ex Juss., Euphorb. Tent. 27, *t.* 7, 1824.

Shrubs or herbs; monoecious (rarely dioecious); stems and foliage with indumentum of bifurcate (malpighiaceous) hairs, often with purplish pigment. *Leaves* alternate; petioles short; stipules small; blades not glandular, entire or dentate. *Inflorescences* short, racemiform, bisexual, with one to several basal ♀ flowers; bracts small, subtending single flowers. *Staminate flowers* with calyx usually 5-lobed, valvate in the bud; petals 5, clawed at base, ± adnate to base of staminal column; disc dissected, segments opposite the calyx-lobes; stamens 5-15, monadelphous, the anthers 1-2(-3) seriate, 1-3 filiform staminodia sometimes present atop the column; pollen grains oblate, tectate, 3- or 4-colporate, bilaterally symmetrical; pistillode absent. *Pistillate flowers* with calyx 5-parted,

the lobes imbricate; petals 5, imbricate, entire, sometimes reduced; disc ± dissected into sometimes elongated segments; ovary of 3 carpels, the ovules 1 in each locule, the styles free or basally connate, bifid, the style-branches ± dilated at the tips. *Fruits* capsular; seeds subglobose, foveolate to reticulate, ecarunculate, endosperm present, the embryo straight, the cotyledons broader than the radicle.

An American genus of about 50 tropical or warm-temperate species, extending from southern U. S. to Argentina. The single Panamanian representative belongs to subg. *Ditaxis* (Vahl ex Juss.) Croizat, a group often treated as a distinct genus because of its biseriate androecium of approximately 10 stamens.

1. **Argythamnia macrobotrys** (Pax & Hoffm.) Ingram, Bull. Torrey Bot. Club **80:** 423, 1953.

Ditaxis macrobotrys Pax & Hoffm., Pflanzenreich **63** (IV, 147, VII): 425, 1914.

Shrub; twigs with pale bark, densely pubescent when young, then glabrate. *Leaves* chartaceous; petioles 3-5 mm long; stipules ca 2-3.5 mm long, triangular, subulate-acuminate; blades lanceolate, 7-10 cm long, 2.5-4 cm broad, sericeous when young, glabrate above, pinnately veined, the base acute, the apex acuminate. *Racemes* 2-4.5 cm long, with 1 or 2 ♀ flowers and 3 or 4 ♂ flowers; rachis strigose; bracts ovate, acute, ca 3 mm long, pilose. *Staminate flowers* with pilose pedicels ca 2 mm long; calyx-lobes narrowly oblanceolate, acuminate, pubescent, 5-5.7 mm long; petals oblanceolate, acute, ca 6-7 mm long, dorsally sericeous, ventrally with sparse indument, exserted beyond the calyx; disc-segments obscure; stamens 10, the anthers biseriate, ca 0.6-0.7 mm long, the staminal column ca 3.5 cm long, the filaments and the 4 or 5 staminodes pilose. *Pistillate flowers* with pedicels 1-2 cm long; calyx-lobes ovate, acuminate, becoming 7-9 mm long, pubescent; petals as in ♂, but shorter than the calyx (ca 4 mm long), pilose; disc-segments thick, glabrous; ovary densely sericeous, the styles ca 1.5 mm long, connate beyond the middle, pilose, bifid, the lobes dilated. *Capsules* (ex Pax & Hoffm., op. cit.) pilose, 6 mm long.

Endemic to Panama.

PANAMA: dry wooded hills, Alhajuela, *Pittier 2360* (type coll. US); Chagres Valley, forests on limestone, *Pittier 3450* (US).

As suggested by the descriptions of Pax and Hoffmann, this species appears to be closely related to the widespread *A. polygama* (Jacquin) O. Ktze., but differs in its longer racemes and narrower ♂ petals. Studies made on a more complete series of collections (including fruiting specimens) are needed to test whether the species is in fact distinct and endemic to Panama.

12. ADELIA

Adelia L., Syst. Nat. ed. 10, 1298, 1759, nom. gen. cons.

Ricinella Muell.-Arg., Linnaea **34:** 153, 1865.

Trees or shrubs; dioecious; twigs often spinescent; indumentum of simple non-glandular trichomes. *Leaves* alternate, petiolate; stipules inconspicuous;

blades pinnately veined, eglandular, entire. *Inflorescences* axillary, glomerulate; flowers apetalous. *Staminate flowers* pedicellate; calyx-lobes 4 or 5, valvate; disc annular, thickened and fleshy; stamens 8-17, monadelphous at least at base (often appearing free in bud), the filaments slender, longer than the anthers; pollen grains 3-4-colpate, tectate, colpi operculate; pistillode minute or obsolete. *Pistillate flowers* long-pedicellate; calyx-lobes mostly 5 or 6, reflexed at anthesis; disc as in ♂; ovary usually of 3 carpels, pubescent, the ovules 1 per locule, the styles free or united at the base, deeply lacerate. *Fruits* capsular, dehiscing to leave a persistent columella; seeds smooth, ecarunculate, the endosperm fleshy, the embryo with broad thin cotyledons and short radicle.

A neotropical genus of about a dozen species, distributed from Mexico and the Bahamas south to Brazil. The Caribbean species are rather difficult to distinguish, and it is possible that some reductions will have to be made. Two species have been reported from Panama, but one of these is known only from a single incomplete collection, and its status is still not clear.

1. **Adelia triloba** (Muell.-Arg.) Hemsley, Biol. Centr.-Amer. Bot. **3:** 130, 1883.—Fig. 11.

Ricinella triloba Muell.-Arg., Linnaea **34:** 153, 1865.
? *Adelia panamensis* Pax & Hoffm., Pflanzenreich **63** (IV, 147, VII): 67, 1914.

Shrub or tree up to 15 m high; dioecious; trunk slender to 2 dm thick; twigs pale, smooth, terete, with inconspicuous lenticels, not spinescent. *Leaves* chartaceous; petioles glabrate, ca 4-9 mm long; stipules lanceolate, inconspicuous, 1 mm long or less; blades elliptic to obovate, mostly 5-20 cm long, 2-7 cm broad, glabrous except for tufts of straight simple hairs in the axils of main veins beneath (rarely entirely glabrous), the major veins ca 5-8 on a side, straight, distinctly raised beneath, the veinlets forming a conspicuous reticulum beneath, the base tapering, narrowly-rounded to subcordate, the margins entire, the apex abruptly cuspidate-acuminate (acumen mostly 1-1.5 cm long). *Inflorescences* glomerulate, several to many flowers of each sex in dense axillary clusters. *Staminate flowers* with slender pubescent pedicels mostly 4-7 mm long; calyx-lobes 5, elliptic, pointed, ca 2-2.3 mm long, pubescent outside; disc fleshy, ca 1-1.3 mm in diam; stamens mostly 13-16, in 2 or more whorls (often 8 or 9 at base, 5 or 6 at the top), the filaments connate into a column ca 0.5-1 mm high, terminated by a pistillode, the filament tips slender, ca 1-1.5 mm long, the anthers blunt, ca 0.4 mm long. *Pistillate flowers* with glabrate pedicels becoming 2-7 cm long in fruit; calyx-lobes 6, lanceolate to linear-lanceolate, blunt or acute, 3-6.5 mm long, pubescent; disc as in ♂; ovary densely pubescent, the styles free, or shortly connate basally, spreading, deeply fimbriate-lacerate, ca (1.2-)1.5-3.5 mm long. *Capsules* trigonous, deeply emarginate-depressed at the top (cocci connate only in lower ½ or ⅔), 7-11 mm in diam, 5.8-7.5 mm high, pubescent; columella slender, ± purplish-tinged, 3-pronged at tip, 3.5-4 mm long; seeds subspheroidal or sometimes distinctly oblate, 3.1-4.1 mm long, 3.4-4 mm in diam, smooth, grayish or waxy-whitened, with distinct raphe.

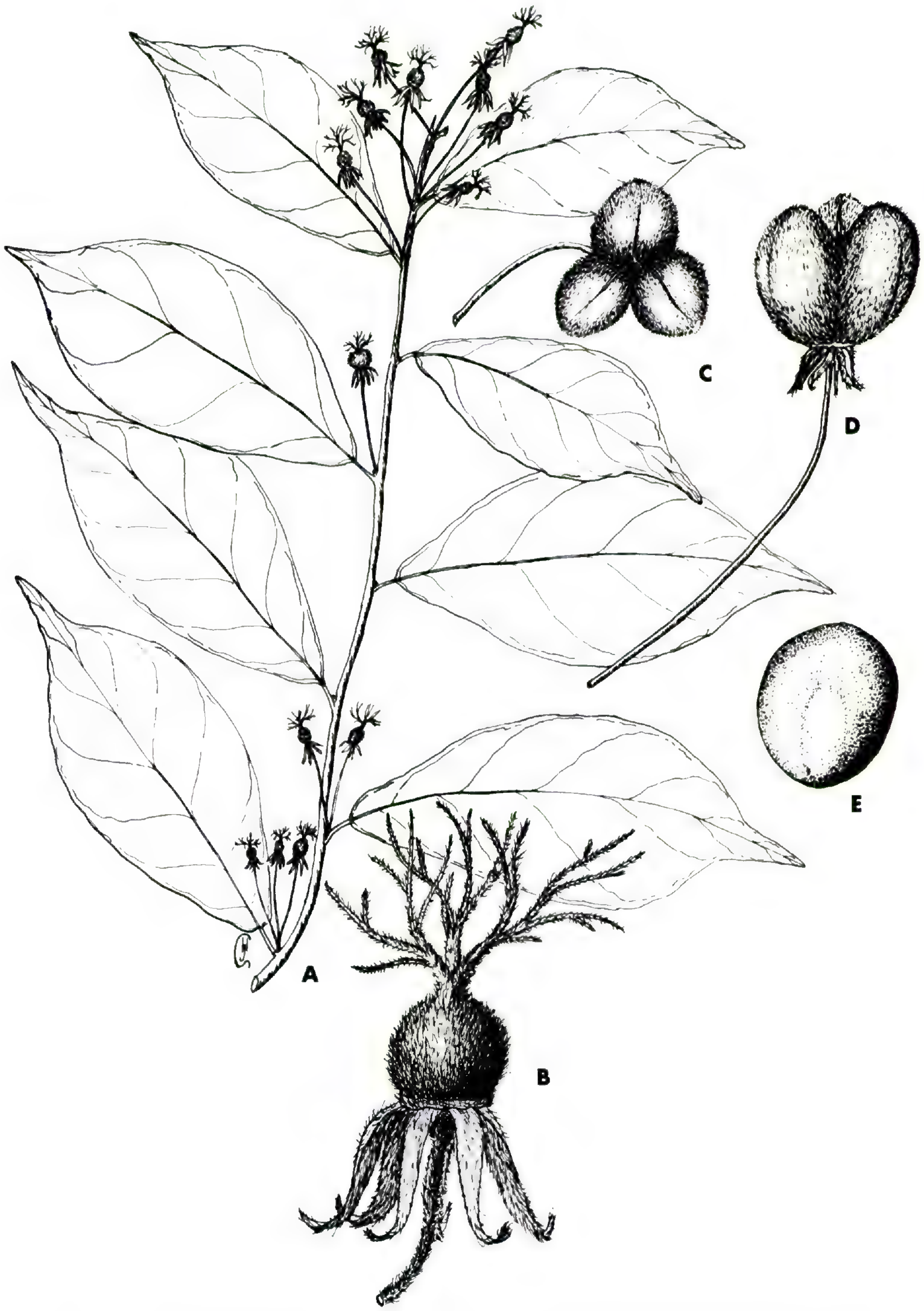

Fig. 11. *Adelia triloba* (Muell.-Arg.) Hemsley: A, habit (×½); B, female flower (×6); C, fruit, top view (×2); D, fruit, side view (×2); E, seed (×4). A-B after *Blum & Dwyer 2106* (MO); C-E after *Tyson 3493* (MO).

Forests, Costa Rica and Panama.

BOCAS DEL TORO: Almirante, Daytonia Farm, *Cooper 394* (F); id., *Cooper 428* (NY, US), *431* (A, F, GH, US); Changuinola Valley, *Dunlap 218* (F, US), *434* (F); Water Valley, *von Wedel 1541* (GH, MO). CANAL ZONE: Barro Colorado I, *Shattuck 748* (F), *806* (F, MO), *Wetmore & Abbe* 35 (A, GH), *145* (GH), *153* (GH), *Wilson 27* (F), *Woodworth & Vestal 510* (A), *522* (A); Cerro Gordo, *Pittier 2313* (US); Darien, *Macbride 2696* (F), *Standley 31549* (US), *31635* (US); Fort Sherman, *Blum & Dwyer 2106* (MO), *Johnston 1735* (GH, MO), *Tyson 2106* (MO); 6 mi N of Gamboa, *Tyson* 3493 (MO); Gorgona to Mamei, *Pittier 2249* (A, GH, US); Las Cascadas plantation, *Standley 25815* (US); vic of Madden Dam, disturbed forest, *Lewis et al. 4* (MO); Mamei, *Hayes 498* (isotype K); Mojinga Swamp, *Allen 869* (MO); Quebrada Melgada, drowned forest and sabanas, *Steyermark 17489* (MO, UC); Río Agua Salud, nr Frijoles, *Piper 5861* (US). COCLÉ: Bismarck, above Penonomé, *Williams 265* (NY, US). DARIEN: Garachiné, forests nr sea, *Pittier 5510* (holotype of *A. panamensis*, US); Marraganti, *Williams 638* (NY). PANAMA: Juan Díaz, *Standley 30509* (US); Juan Díaz to Matías Hernández, *Standley 31962* (US); Río Tapia, *Standley 30687* (US); Río Tocumen, *Standley 29447* (US).

This variable species, which is quite common in disturbed forests in the Canal Zone, is very similar to *A. barbinervis* Cham. & Schl. of Mexico and northern Central America. However, it clearly differs in the characteristically deeply lobed cocci of the fruit, less densely pubescent ovary, and more deeply divided styles.

The status of *A. panamensis*, described by Pax and Hoffmann on the basis of the single Pittier collection from Darien, is still difficult to evaluate. The spinescent branches and small leaves (ca 3-5 cm long) suggest the West Indian *A. ricinella* L., from which the Darien plant would appear to differ in its articulate fruiting pedicels and perhaps larger seeds. However, it should be noted that the spinescent branches and small leaves of Pittier's specimen occasionally occur in otherwise typical *A. triloba* (e.g. in *Standley 30509* from Panama); and one specimen of *A. triloba* (*Allen 869* from Mojinga Swamp) has articulate fruiting pedicels. It is possible, therefore, that *A. panamensis* merely represents an aberrant variant from a drier habitat. The only distinctive character of the taxon not matched in *A. triloba* appears to be the large number of ♀ calyx-lobes (mostly 7-9 vs. 6 in *A. triloba*); but with only a single collection it is impossible to decide whether this feature characterizes a distinct population. Until further collections, including ♂ flowers, can be made in the area it seems best tentatively to regard *A. panamensis* as a local variation of *A. triloba*.

The resemblance of the type collection of *A. panamensis* to the West Indian *A. ricinella* brings up a further perplexing difficulty. Although it differs from *A. triloba* in various tendencies (e.g. more pronounced spininess, smaller leaves and seeds), *A. ricinella* is extremely close overall and not sharply separable by any one character (except possibly the fruit, if the capsules of the West Indian plants, not seen entire, prove not to be deeply trilobed). It might be more reasonable to treat these two taxa as allopatric subspecies of a single species.

13. BERNARDIA

Bernardia Houst. ex P. Browne, Civ. Nat. Hist. Jam. 361, 1756.

Polyboea Kl. in Endl., Gen. Pl. Suppl. IV, **3**: 88, 1850.

Shrubs or subshrubs; monoecious or dioecious; indumentum of simple or stellate hairs. *Leaves* alternate, petiolate or subsessile, stipulate; blades pinnately veined (or trinerved at base), often with basal glands, (usually dentate). *Inflorescences* spike-like, unisexual when monoecious; ♂ flowers in elongate or contracted axillary spikes; ♀ flowers in usually few-flowered axillary or pseudo-terminal spikes; bracts subtending 1 ♀ or several ♂ flowers. *Staminate flowers* sessile or with short pedicels; calyx globose and entire in bud, splitting into 3 or 4 valvate lobes at anthesis; petals absent; disc absent or of minute interstaminal processes; stamens 3-20 or more, the filaments free, erect, the anthers dehiscing vertically; pollen grains 3-colporate, intectate, finely reticulate, colpi narrow and costate; pistillode rudimentary or absent. *Pistillate flowers* sessile; calyx-lobes 4-6, imbricate, small; disc annular or dissected; ovary of 3 carpels, the ovules 1 per locule, the styles short, free, bifid or bipartite. *Fruits* capsular, dehiscent, columella persistent; seeds not carunculate, the endosperm fleshy, the cotyledons broad and flat.

A neotropical genus of 30 to 40 species, most highly developed in Brazil. Several species are known from Mexico, but only two from Panama, and only one other (*B. brandegei* Millsp.) has been reported from Central America.

a. Leaves oblanceolate to obovate, acuminate but not abruptly so, rather finely serrate (teeth ca 30-60 per side); basal foliar glands usually 2, inconspicuous above ..... 1. *B. macrophylla*
aa. Leaves spathulate, abruptly cuspidate-acuminate, remotely serrulate (teeth ca 15-25 per side); basal foliar glands usually 4-6, conspicuous above ..... 2. *B. denticulata*

1. **Bernardia macrophylla** Standley, Jour. Wash. Acad. Sci. **15:** 103, 1925.

Shrub to 3 m high; dioecious; young stems subterete, pubescent with straight, unbranched, mostly antrorse hairs. *Leaves* thin; petioles densely pubescent, 5-10 mm long; stipules subulate-lanceolate, (1-)1.7-2.1 mm long, 0.5-1 mm broad, densely pubescent; blades obovate or oblanceolate, mostly 12-20 cm long, 3.5-7.5 cm broad, with sharp unicellular hairs on both faces, the basal glands usually 2, inconspicuous above, the midrib and veins prominently raised beneath, the primary veins mostly 9-12 on a side, straight, the veinlets at right angles to primaries, the base narrowed, acute, the margins shallowly crenate-dentate, with ca 30-60 teeth per side, the apex acuminate. *Inflorescences* unisexual; ♂ *flowers* in contracted racemes, ♀ flowers in contracted pseudoterminal spiciform racemes. *Staminate flowers* with calyx splitting into 4 or 5 unequal segments; calyx-lobes lanceolate, 3-veined, sparsely pubescent, 1.6-1.8 mm long, 0.7-1.1 mm broad; disc of minute dark clavate interstaminal processes; stamens 14, the filaments free, 0.9-1 mm long, the anthers ca 0.4 mm broad. *Pistillate flowers* sessile; calyx-lobes 5, subequal, ovate, acute, 5-veined, 1.6-1.8 mm long, 0.8-1.3 mm broad, densely pubescent outside; disc thin, cupuliform, 0.25-0.35 mm high, nearly glabrous;

ovary pubescent, the styles bifid, the lobes entire or again bifid, slightly over 0.5 mm long. *Fruits* not seen.

Endemic to Panama.

PANAMA: Río Tocumen, *Standley 29389* (holotype US), *29380* (US), *29471* (US).

By virtue of its penninerved leaves with unbranched trichomes, this species appears to belong in sect. *Polyboea* (Kl.) Muell.-Arg. as defined by Pax [Pflanzenreich **63** (IV, 147, VII): 28, 1914]. Standley compared it with the West Indian *B. corensis* (Jacquin) Muell.-Arg., from which it differs in its larger more pubescent leaves, dioecious inflorescences, and larger stamen number. It is even closer to *B. jacquiniana* Muell.-Arg., which from descriptions scarcely differs except in having fewer stamens (9-12).

2. **Bernardia denticulata** (Standley) Webster, Ann. Missouri Bot. Gard. **54:** 200, 1967.

Cleidion denticulatum Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 218, 1929.

Tree ca 5 m high, trunk 2-2.5 dm thick; twigs antrorsely strigose with simple pointed hairs ca 0.1-0.5 mm long. *Leaves* thinly chartaceous; petioles stout, densely hispidulous, ca 4-10 mm long; stipules not seen, apparently caducous; blades spathulate; 20-26 cm long, 4.8-8 cm broad, smooth and glabrate above with 4-6 shining roundish glands towards the base, sparsely hispidulous-strigose, the midrib and primary lateral veins (ca 7-9 on a side) raised beneath, the veinlet reticulum not very conspiculous, the base evenly tapered, narrowly acute, the margins shallowly and remotely crenulate-serrate, with mostly 15-25 teeth on a side, the tip abruptly short-acuminate. *Pistillate inflorescences* terminal, few-flowered, ca 1-5 cm long; ♂ inflorescences not seen. *Pistillate flowers* with stout sericeous pedicels ca 4 mm long in fruit; calyx-lobes 5, ovate or elliptic, sericeous, 2-2.2 mm long. *Capsules* not seen entire; valves of cocci ca 12-13 mm long, smooth, strigose, the columella dilated into 3 wings, ca 4.5-5 mm high, 7.5-8 mm broad; seeds plump, slightly compressed, not beaked, slightly carinate on the back, mottled dark brown against dark gray, ca 7.8-9.5 mm long.

Known only from the type collection in western Panama.

BOCAS DEL TORO: Chiriquí Trail, Buena Vista Camp, 1250 ft, *Cooper 606* (holotype F; isotypes NY, Y).

The relationships of this species are still somewhat problematical, owing to the incompleteness of the single known collection. If correctly placed in *Bernardia*, the plant probably belongs in sect. *Polyboea*, but is not closely related to *B. macrophylla* nor to any other *Bernardia* in North America.

14. CLEIDION

Cleidion Blume, Bijdr. Fl. Nederl. Ind. 612, 1825.

Trees or shrubs; monoecious or dioecious; with indumentum of simple hairs. *Leaves* alternate, petiolate, stipulate; blades usually dentate, pinnately veined, often with glandular spots at the base. *Inflorescences* axillary, thyrsoid or racemiform; bracts eglandular. *Staminate flowers* ± pedicellate; calyx splitting at anthesis into 3 or 4 valvate lobes; petals and disc absent; stamens numerous (35-80), densely crowded on a convex receptacle, the anthers 4-loculate, connective ± appendaged; pollen grains subglobose, 3-colporate, tectate, psilate; pistillode absent. *Pistillate flowers* pedicellate; calyx-lobes 3-6, imbricate; disc and petals absent; ovary of 3 (rarely 2) carpels, the ovules solitary in each locule, the styles elongated, free, bifid or bipartite. *Fruits* capsular, of 3 (rarely 1 or 2) cocci, the columella slender; seeds roundish, ecarunculate, smooth, endosperm present, the cotyledons broad, thin.

About 20 species, mostly of southeastern Asia and Australasia, with a few species in South America and a single one in Africa. The Panamanian species is the northernmost American representative of the genus.

1. **Cleidion woodsonianum** Croizat, Jour. Arnold Arb. **24:** 167, 1943.

Adenophaedra woodsoniana (Croizat) Croizat, Trop. Woods **88:** 31, 1946.

Tree 4-5 m high; monoecious; twigs minutely scabrid-puberulous. *Leaves* thinly chartaceous; petioles 5-23 mm long; stipules ovate-lanceolate, indurate, ca 1.5-2 mm long; blades elliptic to obovate, 7-13 cm long, 2-4.5 cm broad, minutely pustulate, glabrescent except along the veins (with tufts of hair in vein-axils along midrib), the veins ca 7 or 8 on a side, the veinlet reticulum prominulous beneath, the base cuneately narrowed, the margins crenate-serrate with 14-21 ± callose teeth on each side, the apex ± abruptly caudate-acuminate. *Inflorescences* unisexual, axillary; ♀ racemes 5-15 cm long, rachis slender and minutely puberulous, with 2-5 flowers; ♂ thyrse (only 1 seen) ca 1 cm long, with several flowers crowded at each node. *Staminate flowers* (seen only in bud) short-pedicellate; calyx-segments 3, elliptic, pointed, minutely sericeous-strigose externally; stamens numerous (over 50). *Pistillate flowers* on slender pedicels becoming 10-15 mm long; calyx-lobes 6, biseriate, triangular, acuminate, sericeous, 0.9-1.2 mm long; ovary of 3 carpels, sericeous, the styles ca 2.8 mm long, pubescent, bifid into 2 terete branches. *Capsules* not seen entire, cocci ca 7.5 mm long, smooth, sparsely strigose, the columella slender, not apically dilated, 4.8-5 mm long; seeds roundish, plump, slightly beaked apically, 5 mm long, mottled brown-and-gray.

Endemic to Panama; known only from the type collection.

CANAL ZONE: vic of Salamanca Hydrographic Sta, Río Pequení, ca 80 m, *Woodson et al. 1587* (holotype A; isotypes MO, NY).

15. ALCHORNEA

Alchornea Sw., Prodr. 98, 1788; Fl. Ind. Occ. **2:** 1153, *t. 24,* 1800.

Trees or shrubs; dioecious (in Panamanian species); indumentum of simple or stellate trichomes. *Leaves* alternate, petiolate, inconspicuously stipulate; blades pinnately or palmately veined (often triplinerved), commonly with glandular spots near the base, generally dentate. *Inflorescences* axillary, of spiciform racemes, the ♂ racemes often compound; bracts eglandular, each subtending 1-3 ♀ or 1-several ♂ flowers. *Staminate flowers* subsessile with calyx splitting at anthesis into 2-5 valvate lobes; petals absent; disc central, confluent with bases of stamens; stamens (in local species) usually 8, in 2 whorls of 4, the filaments short, the anthers dehiscing introrsely and longitudinally; pollen grains spheroidal, 3-colporate, colpi operculate; pistillode absent. *Pistillate flowers* sessile to short-pedicellate; calyx-lobes usually 4, imbricate; petals absent; disc obsolete; ovary of 2 carpels, ovules 1 per locule, the styles elongated, free, undivided. *Fruits* capsular, dicoccous, the columella persistent; seeds tuberculate, ecarunculate, with prominent ventral raphe, endosperm present, the cotyledons broad, thin, not curved.

In the narrow circumscription of Pax and Hoffmann [Pflanzenreich **63** (IV, 147, VII): 220, 1914], *Alchornea* comprises about 50 species, the majority of these American. As shown by Punt (Wentia **7:** 82, 1962), *Alchornea* closely resembles such South American genera as *Aparisthmium* and *Conceveiba* in its operculate pollen grains. Critical studies may show, therefore, that Mueller (in DC., Prodr. **15**(2): 899 et seq., 1866) was justified in defining the limits of *Alchornea* broadly.

The available Panamanian collections of *Alchornea* are inadequate to serve as the basis for a satisfactory treatment of the taxa. Four different species appear to be recorded at present, but additional Colombian species may be expected in Darien.

a. Leaves (except on sprout-shoots) not over 20 cm long, glabrescent, with veinlet reticulum moderately prominulous beneath.
  b. Leaves rigidly chartaceous to coriaceous; basal foliar glands mostly 2-4.
    c. Staminate spikes unbranched; leaf vein axils not barbate beneath ..... 1. *A. costaricensis*
    cc. Staminate spikes compound; leaf vein axils distinctly barbate beneath ..... 2. *A. latifolia*
  bb. Leaves membranous to thinly chartaceous; basal foliar glands mostly more than 4 ..... 3. *A. glandulosa*
aa. Leaves 24 cm long or more, stellate-pubescent beneath, with veinlet reticulum corrugate-impressed above and distinctly raised beneath ..... 4. *A. grandis*

1. **Alchornea costaricensis** Pax & Hoffm., Pflanzenreich **63** (IV, 147, VII): 235, 1914.—Fig. 12.

A. costaricensis f. *longispicata* Pax & Hoffm., Pflanzenreich **68** (IV, 147, XIV): 20, 1920.

Tree to 8 or 10 m high, with dense crown; twigs terete, glabrescent. *Leaves* chartaceous; petioles (1-)1.5-4(-9) cm long, pubescent, the hairs straight or sometimes stellate, minute; stipules very inconspicuous, less than 0.5 mm long, tri-

Fig. 12. *Alchornea costaricensis* Pax & Hoffm.: A, habit (ca ×½); B, female flower (×6); C, fruit, top view (×2); D, fruit, side view (×2); E, seed (×4). A-B after *Blum 2106* (MO); C-E after *Tyson 3493* (MO).

angular, pubescent; blades ovate- to elliptic-lanceolate, ca 8-15 cm long, 3-6 cm broad, stellate-pubescent when expanding, at length glabrate, usually with 2 foliar glands between midrib and basal nerves, the major veins mostly 5 or 6 on a side, basal pair nearly straight, prominently raised beneath, glabrate, the base obtuse to rounded, the margins rather sparsely crenulate-dentate (ca 6-10 glandular teeth on a side), the apex distinctly and rather abruptly acuminate (acumen ca 1-2 cm long). *Spikes* stellate-pubescent; ♂ axes unbranched mostly 3-8 cm long, with ca 20-30 nodes, flowers mostly 4-6 per bract; ♀ 2-8(-10) cm long, with mostly 6-15 flowers. *Staminate flowers* subsessile; buds oblate-subglobose, 1.2-1.5 mm in diam; calyx-lobes 3 or 4; stamens with filaments shorter than anthers, confluent with the disc, the anthers oblong or elliptic, ca 0.7-0.8 mm long. *Pistillate flowers* subsessile; calyx ca 1.5 mm high, 4-lobed about ½ way to base, densely pubescent; disc not evident; ovary ellipsoid, densely pubescent, ca 1.5 mm high, the styles distinct, unlobed, tapering to long-attenuate tips, 7.5-10 mm long, 0.7-0.9 mm wide at base, stellate-pubescent on the non-stigmatic portion. *Capsules* obscurely stellate or glabrate, ca 5-6 mm high, 6.5-8.5 mm broad; seeds elliptic, brownish, irregularly tuberculate, 4.8-5.3 mm long, 4.4-4.8 mm broad.

Rain forests, Costa Rica and Panama.

BOCAS DEL TORO: *Carleton 163* (US); Almirante, *Cooper 348* (F, NY, US), *443* (F, NY, US); Changuinola Valley, *Cooper & Slater 103* (F, NY, US), *155* (US), *Dunlap 23a* (MO). CANAL ZONE: *Christophersen 198* (type coll. of f. *longispicata*, US); Barro Colorado I, *Aviles 950* (F), *Kenoyer 660* (US), *Standley 31234* (US), *41006* (US); Fort Randolph, *Standley 28719* (US); Fort San Lorenzo, *Tyson & Blum 3666* (MO); Fort Sherman, *Standley 31039* (US); Madden Dam, *Alston 8904* (BM), *Dwyer & Robyns 18* (MO); Río Paraíso, *Standley 29861* (US); Summit, *Standley 25805* (US); rd to Tortuguilla Cove, *Johnston 1815* (MO).

This species appears to be the most common *Alchornea* in western Panama and the only one in the Canal Zone. Its eastern limit is still undetermined, although the meager available records suggest that it is replaced in Darien by *A. triplinervia* Muell.-Arg. In extreme western Panama (i.e. Bocas del Toro) *A. costaricensis* is sympatric with *A. latifolia*, a species with which it has been much confused in herbaria. The two species may ordinarily be rather easily distinguished vegetatively by texture (stiffer in *A. latifolia*) and leaf pubescence (vein axils barbate beneath in *A. latifolia*); furthermore, the ♂ spikes of *A. costaricensis* are unbranched, in contrast to the compound ones of *A. latifolia*. Probably *A. costaricensis* is actually more closely related to such South American species as *A. glandulosa* Endl. & Poeppig; that species is very similar, although seemingly differing in its thinner leaves with a larger number of foliar glands. Possibly *A. costaricensis* is only a geographical race of the wide-ranging and variable *A. glandulosa*, but until a monographic study can be made, it seems more convenient to maintain it as distinct.

2. **Alchornea latifolia** Sw., Prodr. 98, 1788; Fl. Ind. Occ. **2:** 1154, *t. 24*, 1800; Muell.-Arg. in DC., Prodr. **15**(2): 908, 1866.

Tree ca 5-15 m high; twigs glabrous. *Leaves* coriaceous; petioles nearly or quite glabrous, mostly 2-5 cm long; stipules very inconspicuous; blades ovate or

elliptic, typically 8-20 cm long, 3-8 cm broad (to 30 × 20 cm on sprout-shoots), completely glabrate except for scattered stellate hairs beneath and barbate tufts of long hair in axils of major veins, foliar glands usually 2-4, near base on upper side and often paired on lower side, the major veins ca 5-8 on a side, the basal ones strongly raised beneath, extending nearly or quite half the blade length, the veinlets forming an irregular and usually very distinct reticulum, the base rounded to subcordate, the margins crenate-dentate (typically with 11-14 glandular teeth on a side), the apex obtuse to short-acuminate. *Spikes* axillary; ♂ spikes mostly compound, main axis typically 5-15(-30) cm long, with ca 15-25 nodes, the 4-10 lateral axes ca 0.5-3 cm long; ♀ spikes simple or with 1 or 2 basal branches, 3-20 cm long, with 8-20 flowers. *Staminate flowers* subsessile, ca 1.5 mm broad in bud; calyx-lobes 2-4, ca 1.5 mm long or less, glabrous except for a few apical hairs; stamens 8, the anthers ca 0.7-0.8 mm long. *Pistillate flowers* with pedicels very stout, in fruit ca 1-1.5 mm long and almost as thick, glabrous; calyx-lobes 4, lanceolate, acute or acuminate, ca 2-2.8 mm long, sparsely pubescent; ovary stellate-pubescent, the styles mostly 10-20 mm long. *Capsules* usually dicoccous, 5-7 mm long, 8-10 mm in diam; seeds stramineous, tuberculate, ca 5.8-6.3 mm long, 4.8-5.6 mm broad.

Widespread in the Greater Antilles and much of Central America, mostly in rainforest.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 134* (F, NY, US); Laguna Chiriquí, *Hart 122* (US).

The specimen of Hart is the only 'typical' collection of *A. latifolia* seen from Panama. The collection made by Cooper & Slater is atypical in having leaves with fewer teeth and very narrow bases; however, the prominent vein reticulum and barbate leaf-axils are characteristic of *A. latifolia*. Certain other specimens of *Alchornea* from the Changuinola River valley (especially *Dunlap 23a*) resemble *A. latifolia* in leaf shape but appear to belong in *A. costaricensis* on the basis of most other characters. It seems possible that the 2 species may be hybridizing in western Panama, and intensive field studies there would be of much interest.

3. **Alchornea glandulosa** Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. **3:** 18, *t. 221*, 1841.

Tree to 15 m high; twigs stellate-puberulent. *Leaves* membranous to thinly chartaceous; petioles stellate-puberulent, 1-8 cm long; stipules 0.4-0.6 mm long, basally puberulent; blades elliptic to ovate, ca 5-15 cm long, 3-11 cm broad, early glabrate above, minutely stellate-pubescent beneath especially along the veins, with several (mostly 6-10) elliptical glandular spots near the base above, 3-veined at the base with 1-3 additional pairs of lateral veins, the veinlet reticulum prominulous beneath, the 3 major veins barbate in axils with minor laterals, the base rounded to subcordate, the margins shallowly and remotely serrulate with 6-10 glandular thickened ± incurved teeth on each side, the apex rather abruptly acuminate. *Spikes* stellate-puberulent; ♂ spikes mostly compound, ca 5-14 cm long, mostly with 3-5 lateral axes; ♀ spikes unbranched, 3-10 cm long.

Staminate flowers subsessile, ca 1 mm broad in bud; calyx-lobes 2 or 3, acute, glabrous, less than 1 mm long; stamens 7 or 8, the anthers 0.5-0.6 mm long, blunt. *Pistallate flowers* subsessile; calyx-lobes 4, lanceolate, acute, ca 1-1.5 mm long, pubescent; ovary stellate-tomentulose, the styles stellate-pubescent, mostly 9-11 mm long. *Capsules* and seeds not seen.

Forests, Costa Rica to Venezuela and Peru.

DARIEN: rain forest at crest, Caná-Cuasi trail, *Terry & Terry 1575* (MO).

The identity of the single Panamanian collection is not absolutely certain, as only ♂ flowers are present. The small leaf size suggests the widespread *A. triplinervia* (Spreng.) Muell.-Arg., which is known to reach Colombia, and this collection was in fact cited by Standley and Steyermark (Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 150, 1940) as that species. However, the thinner leaf texture, foliar glands, and small ♂ buds all indicate a probable closer affinity of the Darien plant to *A. glandulosa*.

4. **Alchornea grandis** Bentham, Bot. Voy. Sulphur 164, 1844; Muell.-Arg. in DC., Prodr. **15**(2): 909, 1866.

Tree ca 8 m high, trunk ca 1.5 dm in diam; twigs pubescent. *Leaves* chartaceous; petioles stout, 9-11 cm long, minutely stellate-pubescent; stipules not evident; blades ovate or elliptic, 24-27 cm long, 15-18 cm broad, 3-nerved at base with 3 or 4 additional strong veins on each side of midrib, the veins and veinlets corrugate-impressed above, conspicuously raised beneath; lamina copiously stellate-pubescent beneath, glabrate above, basal foliar glands mostly 2 on each side, plane beneath, raised above, the base rounded to subcordate, the margins shallowly toothed (glandular teeth ca 15-17 on a side) to the base, the tip rounded with an abrupt short acumen. *Spikes* (♀, the ♂ unknown) fascicled 2-4 on nodes below the leaves, 6-12 cm long, with ca 10-15 flowers, rachis densely stellate-pubescent. *Staminate flowers* unknown. *Pistillate flowers* subsessile (pedicels less than 1 mm long); calyx-lobes pubescent, ca 1 mm long or less; ovary stellate-pubescent, the styles 10-15 mm long, very slender, glabrous. *Capsules* (immature) glabrate, ca 7-9 mm in diam.

Forests, Panama and Colombia.

DARIEN: vic of Caná, 1750 ft, *Stern et al. 669* (DAV, GH, MO, US).

Despite the lack of staminate flowers, the characters of the Darien collection agree so well with the descriptions of *A. grandis* that there can be little doubt as to its assignment. This represents a considerable extension of range, since *A. grandis* has heretofore been reported only from the type collection in Colombia (Tumaco, *Hinds s.n.;* K, n.v.), about 400 miles to the south.

16. ALCHORNEOPSIS

Alchorneopsis Muell.-Arg., Linnaea **34:** 156, 1865; in DC., Prodr. **15**(2):764, 1866.

Trees; dioecious; twigs and foliage glabrous or minutely pubescent with simple hairs. *Leaves* alternate, petiolate, exstipulate; blade triplinerved, biglandular at base beneath, the margins entire to remotely crenulate. *Inflorescences* axillary (± fascicled), spiciform; ♂ flowers in glomerules, ♀ flowers solitary at each node; bracts inconspicuous, eglandular. *Staminate flowers* subsessile or pedicellate; calyx splitting at anthesis into 3 or 4 valvate lobes; petals absent; disc massive, hirsutulous; stamens 5-8 (mostly 6), the filaments free, the anthers dehiscing introrsely and longitudinally, the outer locule-halves larger than the inner, with enlarged glandular connective; pollen grains subglobose (slightly oblate), 3-colporate, tectate (psilate); pistillode ± 3-lobed. *Pistillate flowers* pedicellate; calyx-lobes 4 or 5, slightly imbricate; petals absent; disc annular, pulviniform, hirsutulous (± confounded with the base of the ovary); ovary of 3 carpels, the ovules 1 per locule, the styles free, short, recurving, undivided, papillate. *Fruits* capsular, the columella persistent, massive; seeds flattened, ecarunculate, the outer coat fleshy, the inner coat reticulate-striate, the cotyledons broad and thin.

A neotropical genus of three known species, all very similar and questionably distinct. The superficial vegetative resemblance of plants in this genus with *Alchornea* is remarkable, but the indumentum of simple rather than stellate hairs permits their separation even in the vegetative condition. The ♂ inflorescences are similar in both genera, but those of *Alchorneopsis* are never branched, and the ♂ flowers always have a pistillode. The short styles of the ♀ flower of *Alchorneopsis* are very divergent from the elongated ones of *Alchornea,* and the seeds of the two genera are very different. The resemblances between *Alchornea* and *Alchorneopsis* must therefore be ascribed to parallelism, the two genera both having their origin within subtribe *Mercurialinae* but apparently not from an immediately common ancestry. The similarities in anther and seed structure in fact suggest that *Alchorneopsis* may be more closely related to *Tetrorchidium* that to any other neotropical genus of *Euphorbiaceae.*

1. **Alchorneopsis floribunda** (Bentham) Muell.-Arg., Linnaea **34:** 156, 1865; in DC., Prodr. **15**(2): 765, 1866; Pax & Hoffm., Pflanzenreich **63** (IV, 147, VII): 267, 1914.

Alchornea glandulosa Poeppig & Endl. var. ? *floribunda* Bentham, Hooker Jour. Bot. **6:** 331, 1854.

A. nemoralis Martius *η floribunda* (Bentham) Baillon, Adansonia **5:** 239, 1865.

Tree to 20 m high; twigs terete, glabrous or minutely scabridulous. *Leaves* chartaceous; petioles minutely scabridulous, ca 1-5 cm long; blades elliptic, 5-15 cm long, 3-8 cm broad, glabrous except for minute hairs along veins beneath, 3-veined at base, with mostly 2 or 3 additional major veins on either side, the veinlet reticulum prominulous beneath, the basal foliar glands foveate-excavated, the base acute to obtuse, the margins subentire to remotely crenulate, the apex

abruptly pointed or acuminate. *Inflorescences* densely appressed-puberulous; ♂ racemes ca 5-12 cm long, ♀ racemes 2-4 cm long. *Staminate flowers* with puberulent pedicels ca 0.5-1.5 mm long; calyx-lobes 3, sparsely strigose, elliptic, acute, 1.2-1.5 mm long; disc copiously hirsutulous; stamens 5-7 (mostly 6), the filaments glabrous, 1.3-2 mm long, the anthers elliptical, 0.5-0.6 mm long, the prominent connective nearly or quite as long as the anther-sacs; pistillode glabrous, trifid, 0.4-0.7 mm high. *Pistillate flowers* with puberulent pedicels 1-1.5 mm long in fruit; calyx-lobes 3 or 4 [in Panamanian material], ovate, strigose, 0.7-0.9 mm long; disc massive, 1-1.2 mm diam; ovary 1.1-1.3 mm high, pubescent, the styles spreading, coarsely papillate, undivided or obscurely bifid at the tip, ca 0.5 mm long. *Capsules* not seen entire; cocci wrinkled, glabrate, 3-4 mm long, the columella persistent, broadly 3-winged (ovate in outline), 0.7-1 mm high; seeds lenticular (thicker basally), blackish beneath the pale outer coat, striate with discrete or somewhat anastomosing ± discontinuous ribs (ca 10-12 on the back), 2.2-2.5 mm long and broad.

Rain forests, Panama to the Guianas and northern Brazil (Amazonas, Pará).

DARIEN: vic of Caná, 3000 ft, *Williams 782A* (NY).

The single Panamanian collection represents an extension in range limits of *A. floribunda* of more than 800 miles from the type locality on the Rio Vaupés in NW Brazil. The assignment of Williams' specimen to this species must be provisional since it bears only fruits (the above description has been augmented by examination of 3 Brazilian specimens: *Ducke 10292, 13501 18513*; all RB). All 3 species of *Alchorneopsis* are imperfectly known, so that comparisons are difficult. The seed size of the Panama collection is closer to *A. trimera* Lanj. of Surinam than to *A. portoricensis* Urban (which has seeds 3 mm long, fide Pax & Hoffmann). The ♀ calyx of the Panamanian plant, with both 3 and 4 lobes, is intermediate between the 3-merous calyx of *A. trimera* and the 4- or 5-merous calyx of the Brazilian *A. floribunda*. It seems probable that the three 'species' of *Alchorneopsis* are merely geographic races of a single wide-ranging species, but in any event the Panamanian plant can appropriately take the earliest species name in the genus, *A. floribunda*.

17. TETRORCHIDIUM

Tetrorchidium Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. **3:** 23, *t.* 227, 1845.

Trees or shrubs; dioecious (sometimes monoecious ?); branches with simple or malpighiaceous hairs. *Leaves* alternate; petioles usually with stalked glands; stipules glandular; blades pinnately veined, entire to dentate. *Inflorescences* axillary, ♂ flowers in spiciform thyrses, ♀ flowers in racemes (sometimes branched and paniculate). *Staminate flowers* sessile or subsessile; calyx-lobes 3, imbricate, ventrally ribbed; petals absent; disc absent; stamens 3, opposite the calyx-lobes, free, the filaments very short, the anthers extrorse, peltate, 4-loculate; pollen grains 3-colporate, intectate, psilate; pistillode small or obsolete. *Pistillate flowers*

subsessile or pedicellate; calyx-lobes 3, imbricate; petals absent; disc cupuliform or dissected into 3 lobes; ovary of 2 or 3 carpels, ovules 1 per locule, the styles free, short, bifid, the style branches sometimes dilated. *Fruits* capsular, thin-walled; seeds rounded, ecarunculate, the outer seed-coat fleshy, the inner foveolate, endosperm present, the cotyledons broad, flat.

About 15 species, the majority (sect. *Tetrorchidium*) American, but with 5 species [sect. *Hasskarlia* (Baillon) Pax & Hoffmann] in Africa characterized by dense catkin-like staminate spikes. Two allopatric, rather poorly known, species occur in Panama.

Useful reference:

Cuatrecasas, J., The Colombian species of *Tetrorchidium*. Britonia **9:** 76-82, 1957.

a. Basal foliar glands massive (ca 0.5-0.6 mm thick), definitely attached on laminar tissue; leaves mostly 15 cm long or more, with 6 or 7 prominent lateral veins; ♀ flowers subsessile ..... 1. *T. euryphyllum*
aa. Basal foliar glands slender (ca 0.15-0.3 mm thick), attached at junction of lamina and petiole or well down on petiole; leaves 7-12 cm long, mostly with only 4 or 5 prominent lateral veins; ♀ flowers with distinct pedicels mostly 1.5-2 mm long ..... 2. *T. gorgonae*

1. **Tetrorchidium euryphyllum** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 219, 1929.

Tree, to 25 m high with trunk ca 1 dm thick; dioecious. *Leaves* membranaceous or thinly chartaceous, clustered near ends of branches; petioles 1-4 cm long; stipules glandular, ca 1 mm long; blades elliptic to obovate, 14-21 cm long, 6-13 cm broad, minutely strigose-pubescent with malpighiaceous hairs on both faces, the midrib and primary veins (5-6 per side) prominently raised beneath, the veinlets distinctly raised to form a prominent reticulum, the base cuneate, the margins entire but with 1 to 2 cyathiform glands at or above the middle, the apex abruptly short-acuminate. *Inflorescences* axillary; ♂ thyrses 4-8 cm long; rachis densely strigose; ♀ racemes 3-6 cm long, rachis more coarsely yellowish-strigose. *Staminate flowers* subsessile; calyx-lobes fleshy, suborbicular, ca 0.9-1.1 mm long, densely strigose without; stamens apparently adnate to base of calyx-lobes, the filaments indistinct, the anthers cordate-reniform, with broad round connective opposite midrib of calyx-lobe, 0.8-1.1 mm wide. *Pistillate flowers* subsessile (pedicels ill-defined, ca 0.5 mm long, becoming ca 1 mm long in fruit); calyx-lobes ovate-deltoid, ca 1 mm long; disc cupulate, ca 0.8-1 mm high, lobed, enclosing most of the ovary before anthesis; ovary glabrous, 2-locular, the styles dilated, reflexed over the ovary to form a cap ca 0.5-0.7 mm high and 0.8-1.3 mm broad. *Capsules* (immature) ca 5 mm in diam.

Rainforests, Costa Rica and Panama.

BOCAS DEL TORO: vic of Almirante, Buena Vista camp, Chiriquí Trail, 450 m, *Cooper 621* (holotype F; isotypes GH, Y).

2. **Tetrorchidium gorgonae** Croizat [Jour. Arnold Arb. **24:** 170, 1943] subsp. **robledoanum** (Cuatr.) Webster, Ann. Missouri Bot. Gard. **54:** 199, 1967.

T. robledoanum Cuatr., Brittonia **9:** 81, 1957.

Tree or shrub 4-7 m high; dioecious, branches minutely strigose. *Leaves* chartaceous; petioles 0.5-1.5 mm long; stipules triangular, pubescent, ca 1 mm long; blades elliptic to obovate, 7-12 cm long, 3-5.5 cm broad, sparsely strigose with malpighiaceous hairs on both faces, the midrib and primary veins (4-6 on a side) prominently raised on both faces, the veinlets forming a distinct reticulum, the base cuneate, the margins subentire (with 2-4 inconspicuous glandular teeth on each side), narrowed to an abruptly short-acuminate tip. *Inflorescences* axillary; ♂ thyrses 2-6 cm long, rachis densely strigose; ♀ racemes 2-6 cm long, densely strigose. *Staminate flowers* subsessile; calyx-lobes triangular, densely strigose, ca 0.8-0.9 mm long; anthers subsessile, 0.8-0.9 mm wide. *Pistillate flowers* with pedicels 1.3-2 mm long; calyx-lobes ovate, obtuse, strigose, 0.9-1.1 mm long; disc cupulate, 0.8-0.9 mm high, enclosing ½ the ovary or more at anthesis; ovary glabrous, 2-locular, the stylar cap nearly disciform, 0.4-0.5 mm high, 1.2-1.8 mm broad. *Fruits* not seen.

Eastern Panama, Colombia, and (fide Cuatrecasas) Ecuador.

CANAL ZONE: divide betw Río Pina and Río Media, W of Gatun Locks, *Johnston 1688* (MO). PANAMA: Cerro Jefe, *Duke 9415* (MO).

The two collections from Panama unfortunately have only flowers, and fruiting collections are much desired. The plant from the Canal Zone appears to be very similar to the type collection of subsp. *robledoanum* except in its more proximally inserted petiolar glands. The collection from Cerro Jefe has a placement of glands more like that of subsp. *robledoanum*, but it also shows a certain similarity to *T. euryphyllum*. The exact status of all these taxa cannot be resolved until more complete Panamanian collections, with flowers of both sexes as well as fruits, are obtained.

18. CARYODENDRON

Caryodendron Karsten, Fl. Columb. **1:** 91, *t.* 45, 1858.

Centrodiscus Muell.-Arg. in Martius, Fl. Brasil. **11**(2): 325, *t. 102,* 1874.

Trees; dioecious; twigs with simple hairs. *Leaves* alternate, petiolate, stipulate; blades pinnately veined, usually with basal glandular spots, entire. *Inflorescences* unisexual; ♂ flowers in simple or compound terminal spiciform thyrses, ♀ flowers in terminal few-flowered racemes; bracts eglandular. *Staminate flowers* subsessile, several per bract; calyx segments 3, valvate; petals absent; disc massive, pulviniform, central, ± pubescent; stamens 4-7, usually with 1 central in the disc and 1 or 2 whorls of 3 exterior to the disc; the filaments free, abruptly inflexed near the top, the anthers introrse, dehiscing obliquely, connective protrusive; pollen grains subglobose (somewhat oblate), 3-colporate, tectate (tectum perforatum), triangular in polar view; pistillode absent. *Pistillate flowers* with

stout pedicels; calyx-lobes 5 or 6, imbricate; petals absent; disc annular; ovary of 3 carpels (rarely 2 or 4). *Fruits* capsular, the cocci thick-walled, smooth; seeds ovoid to globose, large (over 1 cm long), endosperm present, the cotyledons broad and flat.

Only three known species, the following Panamanian one and two from South America.

1. **Caryodendron angustifolium** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 217, 1929.

Tree 4-6 m high; twigs and foliage glabrous. *Leaves* chartaceous; petioles 1.2-3 cm long; stipules not seen [early deciduous, leaving an oblique scar]; blades elliptic- or oblanceolate-oblong, 19-26 cm long, 5-7 cm broad, with 2-4 glandular spots above near the base, the midrib and main primary veins (ca 6-8 on a side) raised beneath, the veinlet reticulum rather prominent on both sides, the base cuneate, the margins entire, recurved, with a truncate or emarginate acumen at the apex. *Inflorescences* terminal, unisexual; ♂ spike compound, with main axis ca 7 cm long and 4.5 mm broad, bearing 2 lateral axes 8-14 cm long and 2-2.5 mm thick; rachis of ♂ spike minutely antrorse-strigulose, the bracts minutely glandular punctate, subtending bracteolate clusters of several ♂ flowers. *Staminate flowers* [not seen fully expanded] nearly sessile; calyx-segments 3, glabrous, ca 1.5-1.8 mm long; stamens 6 or 7, usually with 1 central, the filaments ca 0.8-0.9 mm high, the anthers ca 0.4-0.5 mm long; disc densely hirsute. *Pistillate flowers* not seen; fruiting pedicel massive (nearly 4 mm thick). *Capsules* not seen entire; cocci ca 2 cm long, 2-2.5 mm thick, densely and closely tomentulose outside, the columella ca 1.7 cm long; seeds spheroidal, smooth, pale brownish, prominently carinate dorsally, obscurely and obliquely costate ventrally, with prominent raphe, 15.8-16.5 mm long, 14.4-15 mm broad.

Endemic to western Panama, on the basis of available records.

CHIRIQUÍ: Progreso, *Cooper & Slater 192* (holotype F 573129). DARIEN: ridge parallel to Río Tucuti, above Tucuti, *Duke 5261* (DAV, MO). LOS SANTOS: road betw Tonosí & Guanico, *Tyson et al. 3126* (MO).

This species is extremely close to *C. grandifolium* (Muell.-Arg.) Pax of Brazil. Standley noted the resemblance, but felt that the Panamanian plant differed specifically in its narrower leaves, smaller flower clusters, and thicker ♂ spikes. Actually, only the latter character seems very impressive. The only floral characters noted which might be diagnostic are the smaller anthers of *C. angustifolium* (0.4-0.5 mm vs. 0.8-0.9 mm; but this might reflect merely the immaturity of Panamanian material examined), and its hirsute floral disc, which is much more densely pubescent than that in the ♂ flower of *C. grandifolium*. Despite the undoubted resemblance of the two taxa, therefore, it seems best to maintain them as distinct species for the time being. *Caryodendron orinocense* Karsten, the original species of the genus, appears to differ in its more highly branched ♀ inflorescence and (if *Ducke 1072*, RB belongs here) larger fruits and seeds.

19. ACIDOTON

Acidoton Sw., Prodr. 84, 1788; Fl. Ind. Occ. 954, 1800, nom. gen. cons.

Gitara Pax & Hoffm., Pflanzenreich **85** (IV, 147, XVII): 187, 1924.

Shrubs or small trees; monoecious or dioecious. *Leaves* alternate, petiolate, stipulate; blades pinnately veined, entire or dentate. *Inflorescences* axillary clusters or racemes; bracts eglandular, subtending solitary flowers. *Staminate flowers* pedicellate or subsessile; calyx-lobes 3-5, valvate; petals absent; disc absent (or confounded with the fleshy receptacle); stamens ca 24-60, the filaments free, glabrous, the anthers extrorse, dehiscing longitudinally, the anther-connective with an apical tuft of stinging hairs; pollen grains ellipsoid, tectate, inaperturate. *Pistillate flowers* pedicellate; calyx-lobes 5-6, narrow, ± imbricate; petals and disc absent; ovary of 3 carpels, pubescent (at least in part) with stinging hairs, the ovules 1 per locule, the styles connate below, spreading above, undivided, strongly papillose. *Fruits* capsular, valves ± armed with stinging hairs; seeds rounded, ecarunculate.

A small Caribbean genus of six species (Jamaica, Hispaniola, Central America, Venezuela). The genus is very closely related to *Tragia*, but differs in its habit and more numerous stamens with the anther-connective terminating in a tuft of stinging hairs.

1. **Acidoton nicaraguensis** (Hemsley) Webster, Ann. Missouri Bot. Gard. **54:** 191, 1967.—Fig. 13.

Cleidion ? nicaraguense Hemsley, Biol. Centr.-Amer. Bot. **3:** 130, 1883.
Gitara panamensis Croizat, Jour. Arnold Arb. **26:** 192, 1945.

Shrub or small tree; dioecious; young branches appressed-hirsute, glabrescent, not spinose. *Leaves* thinly chartaceous; petioles 3-7 mm long; stipules lanceolate, acuminate, ± longitudinally ribbed or striate, 3.5-5.5 mm long; blades elliptic to obovate, ca 10-20 cm long, 3.5-7.5 cm broad, glabrescent except along veins beneath, the midrib and veins (ca 5-8 on a side) distinctly raised beneath, the veinlets prominulous, particularly on underside forming a rather conspicuous reticulum, the base rounded, the margins coarsely crenate-toothed above the middle (ca 4-8 teeth on a side), the apex ± abruptly caudate-acuminate (acumen ca 1.5-2.5 cm long). *Inflorescences* unisexual; ♂ racemes 1-2 cm long, with 7-10 flowers; ♀ racemes becoming 4-6 cm long, with 3-5 flowers; bracts ca 2-3 mm long, acute; inflorescence rachis and bracts strigose-hirsute. *Staminate flowers* with pedicels ca 2 mm long; calyx-lobes 3, lanceolate, pubescent, 3-3.5 mm long; disc not evident; stamens 24-35, free, the filaments glabrous, 1-2 mm long, the anthers ellipsoid, 0.35-0.5 mm long, the apical tuft of stinging hairs ca 0.1 mm long. *Pistillate flowers* with ± recurving pedicels becoming 3-9 mm long; calyx-lobes lanceolate, acuminate, pubescent, ca 1 mm long at anthesis; disc absent; ovary densely pubescent with both stinging and simple hairs, the styles connate into a stout column 1-1.3 mm high, the free style-ends about as long as the column, recurving, densely papillose.

Fig. 13. *Acidoton nicaraguensis* (Hemsley) Webster: A, habit (ca ×½); B, female flower (ca ×6); C, male flower (ca ×8); D, anther (ca ×20); E, dehisced coccus (ca ×3); F, seed (ca ×3). A after *Englesing 141* (MO), Nicaragua; B-D after *Pittier* 6543 (US); E-F after *Duke 8320* (MO).

Capsules not seen entire, valves ca 7 mm long, glabrescent, the columella trifurcate distally, 1.5-1.8 mm high; seeds globose, ca 4 mm in diam.

Forests, Nicaragua and Panama.

DARIEN: s. loc., *Duke 8320* (MO); 2-3 mi S of El Real, *Duke 4851* (DAV, MO, US); forests around Pinogana, *Pittier 6543* (holotype of *Gitara panamensis* A; isotype US).

20. TRAGIA

Tragia L., Sp. Pl. 980, 1753; Gen. Pl. ed. 5, 421, 1754.

Vines (suffruticose herbs or shrubs in extra-Panamanian species); monoecious; with stinging hairs. *Leaves* alternate, petiolate or sessile, stipulate, entire to toothed or lobed. *Inflorescences* bisexual, racemiform, opposite the leaves or terminal on lateral branches; flowers 1-several at proximal nodes; bracts small, subtending solitary flowers. *Flowers* apetalous; calyx 3-6-lobed; disc absent. *Staminate flowers* with articulate pedicels; calyx-lobes valvate; stamens 2-5 (-8), the filaments connate below, the anthers dehiscing longitudinally; pollen grains spheroidal, reticulate, 3-colpate with colpi operculate (rarely inaperturate); pistillode small or absent. *Pistillate flowers* pedicellate; calyx-lobes imbricate; ovary of usually 3 carpels, hispid with stinging hairs, sometimes with dorsal horns, the ovules 1 per locule, the styles united at least at base, unlobed, often papillate. *Fruits* capsular, the columella persistent, with 3 apical points; seeds subglobose, smooth or nearly so, ecarunculate, endosperm present, cotyledons foliaceous.

A variable genus of more than 100 species, about 60 in the New World, but only a single species in Panama. It is easily distinguished from all other local *Euphorbiaceae* by the combination of twining habit and stinging indumentum.

Useful reference:

Miller, K. I., & G. L. Webster, A preliminary revision of *Tragia* (*Euphorbiaceae*) in the United States. Rhodora **69:** 241-305, 1967.

1. **Tragia volubilis** L., Sp. Pl. 980, 1753.—Fig. 14.

T. volubilis ζ *lanceolata* Muell.-Arg. in Martius, Fl. Brasil. **11**(2): 414, 1874.

Twining vine; stems and foliage ± densely covered with stinging hairs. *Leaves* thin; petioles 0.5-2.5 cm long; stipules ovate-lanceolate, acuminate, greenish, ca 2-4 mm long; blades elliptic-oblong, 2.5-7 cm long, 0.7-2.5 cm broad, above sparsely and beneath more densely beset with stinging hairs, mostly 5-veined at base, the base subcordate to distinctly cordate, the margins sharply serrate (teeth 8-20 on a side), the apex acute to acuminate. *Inflorescences* opposite the leaves (sometimes apparently axillary),becoming ca 1-2.5 cm long, usually with a single basal ♀ flower, remaining nodes (ca 15-25) with ♂ flowers; ♀ bracts mostly trifid, ♂ bracts entire. *Staminate flowers* with minutely hispidulous pedicels ca 1.1-1.6 mm long, articulate somewhat below the middle (stumps remaining after dehiscence of flower shorter than to as long as the subtending bract); calyx-lobes 3, elliptic, acute, 0.8-0.9 mm long, 0.5-0.6 mm broad; stamens 2 [in Panamanian specimens], the filaments thick and fleshy, free, shorter than the anthers, the

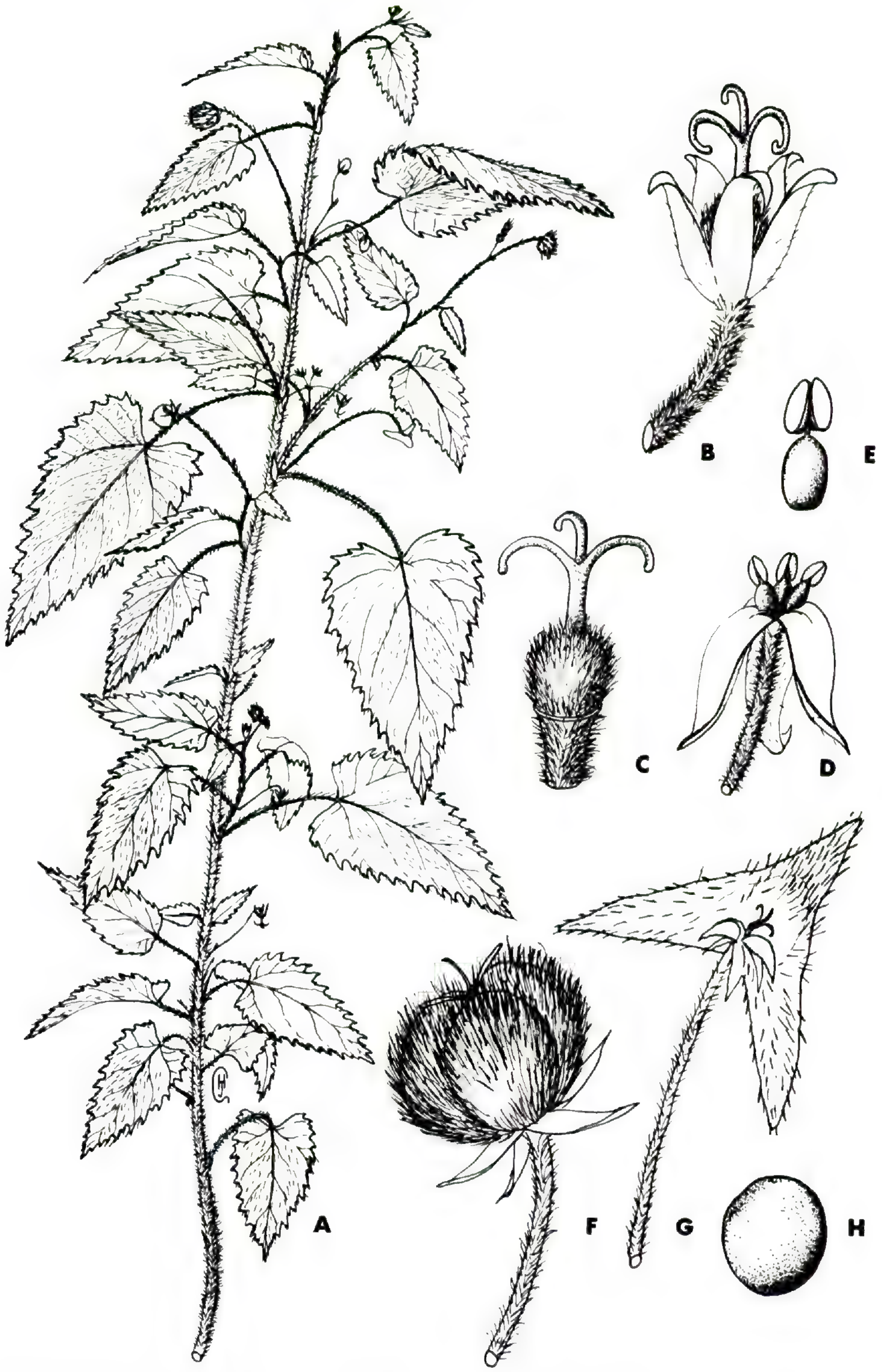

Fig. 14. *Tragia volubilis* L.: A, habit (ca ×½); B, female flower (ca ×10); C, ovary (ca ×10); D, male flower (ca ×20); E, stamen (ca ×30); F, normal 3-coccus fruit (ca ×4); G, fruit with prominent horns (ca ×4); H, seed (ca ×4). After *Lewis et al. 1653* (MO).

anthers elliptic, 0.3-0.4 mm long. *Pistillate flowers* with hispidulous pedicels which elongate greatly in fruit to (1-)1.5-2.5 cm long; calyx-lobes 6, ± biseriate, lanceolate, acute, greenish, reflexed in fruit, increasing from ca 1.2 to ca 1.8 mm in length; ovary densely hispidulous with stinging hairs, the styles basally connate into a column 0.4-1.2 mm high, the tips spreading or usually tightly inrolled. *Capsules* hispid with stinging hairs, dimorphic, some of the normal 3-coccous type and ca 6 mm in diam, others zygomorphic, with 2 prominent dorsal horns up to 4 mm long, the columella slender, apically dilated into 3 flattened blades, 1.6-1.8 mm long; seeds round, ellipsoid, grayish with reddish-brown ridges (alveolate-reticulate, the color contrast lost in age), ca 2.5 mm long.

Common and widespread in tropical America from Mexico and Cuba south to Peru, Argentina, and Uruguay; also reported from Africa (where it is presumably introduced).

CANAL ZONE: Balboa, moist thickets, *Standley 25472* (US), *26051* (US), *27173* (US); betw Corozal & Ancon, *Pittier 6741* (US). HERRERA: secondary woods, 12.5 mi S of Ocú, *Lewis et al. 1653* (DAV, GH, MO, US).

Although Pax and Hoffmann [Pflanzenreich **68** (IV, 147, IX): 50, 1919] reported var. *lanceolata* from Panama (on the basis of *Williams 549,* n.v.), the specimens examined by me have distinctly serrate leaves and accord well with the typical variety. The plant is doubtless much more widely distributed in Panama than the herbarium records indicate, but has evidently been avoided by most collectors.

21. PLUKENETIA

Plukenetia L., Sp. Pl. 1192, 1753; Gen. Pl. ed. 5, 438, 1754.

Lianas; young stem apices puberulent with simple hairs. *Leaves* alternate, petiolate, stipulate (stipules small and deciduous); blades entire or dentate, palmately or pinnately veined, usually stipellate and with a pair of sessile glands at base. *Inflorescences* axillary, narrowly paniculate or thyrsoid, ☿ or ♂; ♀ flowers 1 or 2 at the base of ☿ inflorescences, ♂ flowers in ± abbreviated distal monochasia; bracts small, eglandular. *Staminate flowers* pedicellate; calyx splitting into usually 4 lanceolate segments; petals absent; receptacle slightly to distinctly conical; disc of interstaminal segments or absent; stamens 10-40, the filaments free or ± basally adnate to the receptacle, the anthers ± 4-lobed, apiculate; pollen grains oblate, 3-colpate, tectate; pistillode rudimentary or absent. *Pistillate flowers* with stout pedicels; calyx-segments 4 or 5, barely imbricate; petals and disc absent; ovary of 3 or 4 carpels, ovules solitary in each locule, the styles connate at least half way, the style-tips entire or obscurely bilobed. *Fruits* large, capsular, cocci smooth to carinate or winged, rather thick-walled; seeds globose to lenticular, smooth, ecarunculate, endosperm present, the cotyledons ovate, palmately veined.

In the broad circumscription of Bentham (Gen. Pl. **3:** 327, 1880), this is a rather variable genus of about 15 species from tropical regions except Australia. Proposed segregate genera such as *Anabaenella, Angostylidium, Apodandra,*

Elaeophora, *Fragariopsis*, and *Pterococcus* are each distinguished by only one or two characters, whereas they all have much in common with the typical element (*Plukenetia volubilis* L.) in habit, flowers, pollen, and fruits. Since these segregate taxa each have only one to three species, the utility of fragmenting the *Plukenetia* complex to such an extent seems questionable.

1. **Plukenetia volubilis** L., Sp. Pl. 1192, 1753; Pax & Hoffm., Pflanzenreich **68** (IV, 147, IX): 14, 1919.—Fig. 15.

P. peruviana Muell.-Arg., Linnaea **34**: 157, 1865.

Liana; twigs minutely appressed-pubescent, glabrescent. *Leaves* membranous; petioles mostly 3-8 cm long; stipules brownish, glabrous, ovate-lanceolate, 1-1.5 mm long; blades ovate, ca 7-13 cm long, 5-12 cm broad, glabrate and shining above, glabrate or sparsely hirsutulous and paler beneath, ventrally with 2 prominent ellipsoidal shining marginal glands (ca 1.5-2 mm long) near the base, major veins at base of blade 3, the remainder of blade pinnately veined (3 or 4 major laterals on either side), the veinlet reticulum conspicuous, the base truncate to subcordate, the margins finely to rather coarsely denticulate, the apex abruptly caudate-acuminate. *Inflorescences* axillary, ☿, ca 3-8 cm long at anthesis, becoming up to 15-20 cm long in fruit; ♀ flowers solitary at lowermost nodes, ♂ flowers in clusters at distal nodes. *Staminate flowers* with pedicels ca 1-1.5 mm long; calyx-segments generally 4, lanceolate, acute, 1.8-2.5 mm long; receptacle conical, 0.7-1.5 mm high; disc obsolete; stamens 19-24, inserted spirally on the receptacle, the filaments 0.3-0.6 mm long, the anther-sacs bipartite, the locules discrete (hence anthers 4-partite), 0.3-0.4 mm long, the connective apex blunt and glandular. *Pistillate flowers* with pedicels becoming 10-15 mm long; calyx-lobes oblong-lanceolate, 1.8-2 mm long, 0.9-1 mm broad; ovary of 4 glabrous carinate carpels, the stylar column 11-25 mm long, slender, the stigmas thick, bilobed. *Capsules* deeply 4-lobed, oblate, up to ca 2 cm high, 3.5 cm broad, the cocci thick and rigid; seeds lenticular with thinner margins, reticulate-venose, brownish-mottled, 15-17 mm broad.

Lowland rain forests below 1000 m, Lesser Antilles and Panama south to Peru, Bolivia, and Brazil.

LOS SANTOS: betw Los Santos & Guarare, in thickets, *Woodson et al. 1201* (A, MO, NY).

The single Panamanian collection bears only small (immature?) fruits, and the above description has been augmented by reproductive details from some extra-Panamanian specimens (Ecuador, *Mexia 7309;* Bolivia, *Krukoff 10082, Steinbach 7352;* all UC). Although the collection from Los Santos accords reasonably well with South American material of *P. volubilis* L., more complete Panamanian collections are needed in order to make the identity of our representative a certainty.

Fig. 15. *Plukenetia volubilis* L.: A, habit (ca ×½); B, male flower (ca ×8); C, female flower (ca ×2). A after *Mexia 6470* (MO), Peru; B-C after *Klug 3901* (MO), Peru.

22. OMPHALEA

Omphalea L., Syst. Nat. ed. 10, 1264, 1759, nom. gen. cons.

Hebecocca Beurl., Svensk Vet. Akad. Handl., 1854, 146, 1856.

Shrubs, lianas, or small trees, with clear latex; monoecious. *Leaves* alternate (sometimes approximate at ends of branches), distinctly petiolate, stipulate; blades large, pinnately veined but often 3-nerved at base, entire to deeply lobed, usually with 2 large glands at junction with petiole. *Inflorescence* paniculate (a compound thyrse); floral bracts often conspicuous and foliose; cymules ♂ or ☿. *Staminate flowers* short-pedicellate; calyx-lobes 4, decussate (rarely 5 and imbricate); petals absent; disc patelliform, fleshy, entire; stamens 2 or 3, the filaments connate, the connectives of anthers connate into a large fleshy disciform mass with anthers at

the periphery, the anthers dehiscing obliquely; pollen grain oblate, 3-colpate, tectate (psilate); pistillode absent. *Pistillate flowers* short-pedicellate; calyx-lobes 4 (rarely 5); petals absent; disc annular, sometimes indistinct; ovary of 3 carpels, with 1 ovule in each locule, the styles connate into a stout column which is entire or barely 3-lobed at the apex. *Fruits* fleshy but ultimately dehiscing into 3 1-seeded woody cocci; seeds subglobose, ecarunculate, endosperm present, the cotyledons broad, cordate at base.

A primarily American genus of 15 species, most of these in the West Indies, only three species known from the Old World. Most of the American species are known from very few collections, and careful field work is still needed to determine whether there are significant differences in fruit characters, etc. In addition to the one species known from Panama, two others have been described from Central America by Hemsley. The relationships between these taxa remain to be carefully investigated.

1. **Omphalea diandra** L., Sp. Pl. ed. 2, 1377, 1763; Muell.-Arg. in DC., Prodr. **15**(2): 1135, 1866; Pax & Hoffm., Pflanzenreich **52** (IV, 147, V): 20, 1912.—Fig. 16.

O. diandra var. *panamensis* Kl. in Seemann, Bot. Voy. Herald 101, 1853.
Hebecocca panamensis Beurl., Svensk. Vet. Akad. Handl., 1854 (Prim. Fl. Portob.) 146, 1856.
Omphalea panamensis (Beurl.) I. M. Johnston, Sargentia **8**: 177, 1949.

Liana up to 30 m high; main stems 5 cm thick or more; bark exuding reddish or purplish sap when cut. *Leaves* firmly chartaceous; petioles (1-)2-11 cm long; stipules ca 2-2.5 mm long, pubescent; blades elliptic to oblong, ca 8-21 cm long, 5-15 cm broad, pubescent beneath or sometimes glabrate, the veins at base 3 or 5, with 2 or 3 additional pairs of main veins, the veinlet reticulum conspicuous beneath, the glands at base of blade massive, rounded, sessile, ca 1.2-2 mm wide, the base rounded to truncate or subcordate, the margins entire, the apex mostly bluntly obtuse. *Inflorescences* paniculate, ca (1-)2-5 dm long, with a few lateral axes toward the base, these ca 1-15 cm long, sometimes again branched, bearing many ♂ and a few ♀ flowers which are central in ☿ cymules or solitary at ends of ultimate axes; bracts on lower parts of axes lanceolate, densely pubescent, 2-3 mm long, biglandular near the base; bracts on distal parts of axes foliose, ca 2-3.5 cm long, 1.5-5 mm broad, glabrate, biglandular well above the base (ca 4-8 mm). *Staminate flowers* with pedicels becoming 1.5-2.5 mm long; calyx-lobes 4 (rarely 5), biseriate, unequal, the inner pair ± cochleately enveloping the androecium, fleshy, at anthesis 1.5-2.7 mm long, 1.7-2.6 mm broad, glabrous except for the ± ciliate margins; disc fleshy, ± adnate to base of calyx-lobes, ca 1.5-2.2 mm across; stamens 2 (rarely 3), the androecium (dilated connectives) disciform, fleshy, 1-1.5 mm wide, the anthers 0.6-0.8 mm long. *Pistillate flowers* on pedicels ca 1-2 mm long; calyx-lobes 4 and decussate (rarely 5), ovate, fleshy, 1.5-2 mm long and about as broad, pubescent or nearly glabrous; disc thin, circular, ca 1.2 mm wide, hidden under the ovary; ovary ca 3-4 mm high, ovoid, sericeous, the stylar column stout, sericeous, 2-2.5 mm long, the stigmas erect, ca 0.2 mm long.

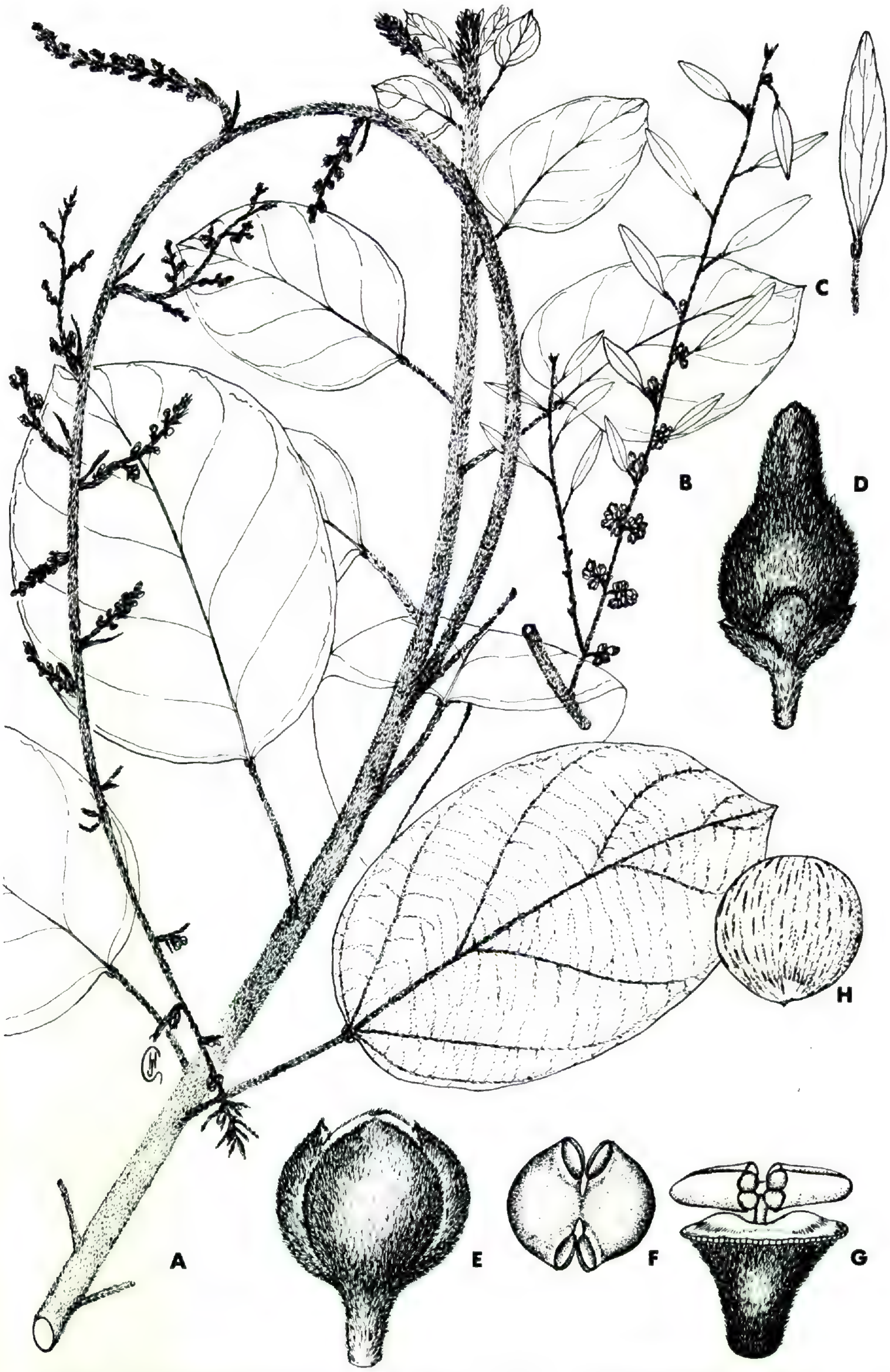

Fig. 16. *Omphalea diandra* L.: A, habit (ca ×½); B, inflorescences (ca ×½); C, inflorescence bract (ca ×1); D, female flower (ca ×6); E, male flower (ca ×4); F, stamens, top view (ca ×10); G, stamens, side view (ca ×10); H, seed (ca ×½). A after *Duke 4906* (MO); B-G after *Wright 1990* (MO), Cuba.

Fruits fleshy, pomiform, ca 8-12 cm in diam, at length dehiscent (?); seeds compressed, rounded, 3.9-4.5 cm broad, brown, rugulose.

West Indies to South America (Peru and Brazil), usually in lowland rain forests or swamp forests; present in Central America along the Caribbean lowlands from Honduras to Panama.

BOCAS DEL TORO: Old Bank I, vic of Chiriquí Lagoon, *von Wedel 1921* (GH, MO). CANAL ZONE: Barro Colorado I, *Aviles 22b* (F), *Bangham 504* (A, F), *Shattuck 619* (F), *Wetmore & Woodworth 58* (A), *Woodworth & Vestal 613* (A); Fort Randolph, *Standley 28645* (US); beach thicket, vic of Fort Sherman, *Standley 30921* (US), *31191* (US); Lion Hill Sta, *Hayes 660* (BM, K). DARIEN: Cativo Swamp, 5 mi downstream from El Real, *Duke 4906* (MO); along Río Tuira below El Real and Piriaque I, *Stern et al. 889* (MO). PANAMA: San José I, West Loop Rd, *Erlanson 110* (GH); id., Long Beach, *Johnston 599* (GH), *1183* (GH, MO); id., Playa Grande, *Johnston 720* (GH). VERAGUAS: Isla Coiba, *Dwyer 1622* (DAV, MO), *Seemann 635* (possibly an isotype of var. *panamensis,* BM).

Johnston (Sargentia **8:** 177, 178, 1949) has presented a valuable description of the plant as it occurs on San José Island. However, his decision to separate the Panamanian plants as a species separate from *O. diandra* is not convincing. As Klotzsch noted in the original description of his variety *panamensis,* the leaf shape of *O. diandra* is quite variable. Seemann's specimen has floral bracts which are about as long as those found in plants elsewhere, and its inflorescence is similar also. Perhaps the Panamanian population does represent a reasonably distinctive geographic race characterized by glabrate leaves with blunt tips and usually only 3 prominent veins at base. Until the genus is monographically revised, it can be conveniently referred to as *O. diandra* var. *panamensis* Kl.

23. RICINUS

Ricinus L., Sp. Pl. 1007, 1753; Gen. Pl. ed. 5, 437, 1754.

Shrubs or trees (in tropical regions); twigs and foliage glabrous, sap watery. *Leaves* alternate, petiolate (petioles long, ± glanduliferous at apex), stipulate (stipules fused into a caducous sheath); blade peltate, palmately 7-11-lobed, serrate. *Inflorescences* terminal (sometimes appearing opposite the leaves or axillary due to sympodial growth), paniculate, the proximal nodes with cymules of several ♂ flowers, the distal cymules ♀ or ☿; bracts papery, glandular at base; the flowers with valvate calyx, apetalous, disc absent. *Staminate flowers* pedicellate; calyx calyptrate in bud, splitting into 3-5 segments at anthesis; stamens ∞ (up to 1000), the filaments partially connate into fascicles at base, irregularly branched; pollen grains spheroidal, tectate, 3-colporate, colpi narrow; pistillode absent. *Pistillate flowers* pedicellate, with calyx similar to the ♂; ovary of 3 carpels, muricate, the ovules 1 per locule, the styles connate below, bifid, the branches usually conspicuously papillate. *Fruits* capsular, echinate (or smooth in some cultivars), the columella wing-dilated above; seeds elliptic, somewhat compressed, smooth, mottled, carunculate, the endosperm copious, the cotyledons foliaceous and palmately veined.

A monotypic genus native to the Old World; probably African in origin, but now widely distributed in tropical and warm-temperate regions.

Ricinus communis L., Sp. Pl. 1007, 1753.

Shrub or tree, usually 2-5 m high; twigs (in most varieties) glaucous. *Leaves* thin, glabrous; petioles 1-2 dm long or more, the gland at apex of petiole on dorsal side of blade, single or sometimes paired, patelliform, dark, subsessile, ca 2-3 mm across; stipules ca 1-1.5 cm long, caducous, leaving a prominent annular scar; blades mostly 7-9-lobed, ca 1 dm across or more (up to 1 m), peltate, the lobes lanceolate, acuminate, pinnately veined, the margins serrate with ± glandular teeth. *Panicles* terminal, bisexual, the 3-10 lowermost nodes with clusters of several ♂ flowers, the distal nodes ♀ (a few intermediate nodes often ☿); bracts papery, associated with dark patelliform glands. *Staminate flowers* with articulate pedicels ca 5-15 mm long; calyx-lobes lanceolate, acute, ca 4-9 mm long; androecium ca 5-7 mm wide, the anthers 0.3-0.4 mm long. *Pistillate flowers* with pedicels becoming mostly 1.5-3 cm long in fruit; calyx-lobes mostly 5, lanceolate, acute, ca 3-4 mm long, persistent or deciduous; ovary coarsely muricate, the styles bifid or bipartite, reddish, densely papillose, ca 3-4 mm long. *Capsules* ordinarily echinate, 12-21 mm in diam, the columella wing-dilated distally, ca 1 cm long or more; seeds ellipsoidal, somewhat flattened, diversely mottled, 9-22 mm long, 4.5-9 mm broad.

Native probably of Africa; cultivated in Panama (as elsewhere in the tropics) and tending to escape in highly disturbed areas.

COLÓN: Gatun Lake, Goodyear Estate, *Seibert 1521* (MO). LOS SANTOS: Pocri, bridge at Río Purio, *Dwyer 2456A* (MO).

24. ACALYPHA

Acalypha L., Sp. Pl. 1003, 1753; Gen. Pl. ed. 5, 436, 1754.

Herbs, shrubs, or rarely trees; monoecious or dioecious; indumentum of simple hairs or glands. *Leaves* alternate, petiolate, stipulate; blades pinnately or palmately veined, undivided, entire or dentate. *Inflorescences* spicate, terminal or axillary; spikes unisexual or bisexual; ♂ flowers several at each node, subtended by a minute bract; ♀ flowers 1-3 at each node, subtended by a usually large foliaceous, lobed bract; the flowers apetalous, disc absent. *Staminate flowers* subsessile; calyx parted into 4 valvate segments; stamens 4-8, the filaments free or basally connate, the anther-sacs pendent, unilocular, elongated and vermiform; pollen grains oblate-spheroidal, 3-5 pseudoporate, tectate, psilate; pistillode absent. *Pistillate flowers* subsessile (pedicellate in a few species); calyx-lobes 3-5, imbricate; ovary of 3 (rarely 1 or 2) carpels, the ovules solitary in each cell, the styles free or basally connate, several times divided into filiform segments (rarely bifid or entire). *Fruits* capsular, sometimes surrounded by the accrescent ♀ bract; seeds ovoid, usually carunculate, smooth to pitted or tuberculate, endosperm present, the embryo straight.

A homogeneous genus of some 400 species, the majority American. The greatest concentration of species is in the Caribbean region, but Panama is rather poorly represented. In addition to the nine native species enumerated below, at least one

other is represented by a single ♂ collection from Darien (Río Balsa, *Duke* 8795, MO). Although its identity is uncertain in the absence of ♀ flowers, it may prove to be *A. cancana* Muell.-Arg. (in DC., Prodr. **15**(2): 869, 1866), described from northwestern Colombia. The plant resembles *A. macrostachya* but is easily distinguished by its more velutinous pubescence and more slender ♂ spikes.

Cultivated plants of *A. wilkesiana* Muell.-Arg. and *A. hispida* Burm. f. may be found in the Canal Zone and elsewhere, but neither species appears to have become naturalized.

a. Pistillate flowers pedicellate, the minute subtending bracts not becoming foliaceous (subg. *Linostachys*)
  b. Pistillate inflorescences terminal, paniculate; leaves without resinous dots beneath ..... 1. *A. costaricensis*
  bb. Pistillate inflorescences axillary, racemose; leaves with minute resinous dots beneath ..... 2. *A. villosa*
aa. Pistillate flowers sessile, the subtending bracts becoming conspicuous and foliaceous (subg. *Acalypha*)
  c. Herbs or shrubs; ♀ bracts with rounded to acute or short-acuminate tips.
    d. Shrubs; spikes all axillary.
      e. Leaves palmately veined at base; ♀ bracts with 10-25 acute lobes, subtending solitary flowers; spikes mostly unisexual.
        f. Pistillate spikes with 15-65 bracts; ♀ bracts in fruit 5-8 mm long, shallowly toothed (lobes cut ca 1/3 to 1/5 way to base); ♂ spikes 3-5 mm thick; capsules smooth ..... 3. *A. macrostachya*
        ff. Pistillate spikes with 1 or 2 bracts; ♀ bracts in fruit 4 mm long, more deeply toothed (lobes cut ca 1/2 way to base); ♂ spikes less than 2 mm thick; capsules verruculose ..... 4. *A. leptopoda*
      ee. Leaves pinnately veined; ♀ bracts subentire, subtending 2 or 3 flowers; spikes mostly bisexual, with 1 or 2 ♀ bracts at base; capsules verruculose ..... 5. *A. diversifolia*
    dd. Herbs; ♀ spikes terminal, ♂ axillary; ♀ bracts obtusely 5-7 lobed ..... 6. *A. septemloba*
  cc. Herbs; ♀ bracts 3-12 lobed, the lobes terminating in long green aristate tips.
    g. Pistillate or ☿ spikes terminal (at least in part); leaves acuminate.
      h. Pistillate bracts 2-flowered, glabrous; styles laciniate; seeds 2.5-2.8 mm long; stipules at least 10 mm long ..... 7. *A. polystachya*
      hh. Pistillate bracts 1-flowered, densely hispid; styles unbranched; seeds 1-1.1 mm long; stipules less than 2 mm long ..... 8. *A. alopecuroidea*
    gg. Spikes all axillary; leaves acute stipules 1.5-2.5 mm long; ♀ bracts 1-flowered, hispid; styles 3-5-lobed ..... 9. *A. arvensis*

1. **Acalypha costaricensis** (O. Ktze.) Knobl. ex Pax & Hoffm., Pflanzenreich **85** (IV, 147, XVI): 16, 1924.—Fig. 17.

Ricinocarpus costaricensis O. Ktze., Rev. Gen. Pl. **2**: 615, 1891.

Shrub 0.5-4 m high; monoecious or dioecious; stems greenish, glabrate to sparsely appressed-hirsutulous. *Leaves* membranous; petioles (1.5-)3-8 cm long, sparsely strigose to glabrate; stipules lanceolate, pubescent, flat, dark, 2.5-3.5 mm long; blades elliptic to slightly obovate, mostly 8-23 cm long 3.5-12 cm broad, glabrous (except along veins) and minutely pustulate, 3-nerved at base but other-

Fig. 17. *Acalypha costaricensis* (O. Ktze.) Knobl.: A, habit (ca ×½); B, female flower (ca ×7); C, fruit (ca ×8); D, seed (ca ×8). A after *Yuncker et al.* 8463 (MO), Honduras; B-D after *Godfrey* 66583 (MO), Costa Rica.

wise pinnately veined (veins 8-10 on a side), the narrowed base rounded to truncate, the margins coarsely dentate (12-25 teeth on a side), the apex acuminate. *Inflorescences* unisexual; ♀ flowers in terminal compound racemes (panicles) 10-25 cm long, with ca 15-35 lateral branches, the longer of these 3-7 cm long; ♂ flowers in axillary spikes mostly 5-20 cm long, ca 1.5-2.5 mm thick, peduncles ca 1 cm long or less. *Pistillate flowers* solitary; bracts linear-lanceolate, acuminate, pubescent, ca 0.5-1 mm long, pedicels 0.5-1 mm long at anthesis; calyx-lobes 5, lanceolate, 0.9-1.2 mm long; ovary densely and prominently verrucose-hispidulous, the styles free, basally thickened, 1.3-2 mm long, distally laciniate into 5-10 narrow segments. *Capsules* ca 3 mm broad, densely verrucose with cylindrical dark purplish processes; seeds plumply ovoid (nearly globose), slightly beaked apically, light brown, smooth (minutely foveolate), 1.6-1.8 mm long, the caruncle small (ca 0.1 mm long) or obsolete.

Lowland rain forests, below 1000 ft, Honduras to Panama.

BOCAS DEL TORO: vic of Changuinola, *Lewis et al. 808* (GH, K, MO, NY, UC, US); 10-15 mi S of mouth of Changuinola River, *Lewis et al. 989* (MO); vic of Chiriquí Lagoon, *von Wedel 1014* (GH, MO, US), *1031* (GH, MO, US); id, Shepherd I, *von Wedel 2687* (GH, MO, US); id, Water Valley, *von Wedel 618* (GH, MO), *1784* (GH, MO, US); PANAMA: Las Delicias, *Carleton 44* (GH, US).

2. **Acalypha villosa** Jacquin, Enum. Syst. Pl. 32, 1760; Sel. Stirp. Pl. Amer. 254, *t. 183 f. 61*, 1763; Hort. Vindob. **3:** 26, *t. 47*, 1776.

Shrub or small tree 2-8 m high; monoecious or dioecious; stems villose with ± appressed hairs. *Leaves* with slender villose petioles 3-12 cm long; stipules linear-lanceolate to subulate, pubescent, 2.5-4 mm long; blades membranous, ovate to ovate-lanceolate, acuminate, mostly rounded to subcordate at the base, generally 8-15 cm long, 5-9 cm broad, above strigose or glabrate, beneath sparsely to densely villose and dotted with small (0.05-0.1 mm) shining resinous droplets, 5-nerved at base but pinnately veined above (veins ca 6-8 on a side), the margins coarsely crenate-dentate (25-35 teeth on a side). *Inflorescences* unisexual, axillary; ♀ flowers in slender racemes ca 5-15 cm long, with ca 10-40(-60) flowers, short pedicellate; ♂ flowers in spikes ca 3-8 cm long, 1-2 mm thick, rather loosely flowered and becoming ± interrupted proximally, sessile or with peduncles ca 1-2.5 cm long. *Pistillate flowers* solitary; bracts very small, scarcely more than 0.5 mm long, pubescent; pedicels 1-1.3 mm at anthesis, attaining 1-3 mm in fruit; calyx-lobes 5, lanceolate, 0.6-0.8 mm long, pubescent; ovary densely verrucose and dotted with resinous droplets, the styles free, basally verruculose, 2-2.5 mm long, distally laciniate into ca 5-10 narrow segments. *Capsules* ca 2 mm broad, densely verrucose with greenish processes and hispidulous; seeds plumply ovoid (nearly globose), slightly beaked apically, light brown, smooth (minutely foveolate), ca 0.9-1.1 mm long, the caruncle nearly obsolete.

A widespread and polymorphic species, from British Honduras south to Brazil and Paraguay.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 405* (US); vic of Chiriquí Lagoon, Shepherd I, *von Wedel 2686* (GH, MO). CANAL ZONE: Fort Kobbe, nr beach, *Duke 4222* (DAV, MO). CHIRIQUÍ: Río Chiriquí to Remedios, *Woodson et al. 1194* (A, MO). PANAMA: Taboga I, *Dwyer 2840* (DAV, MO), *Pittier 3547* (US), *Riley 139* (MO), *Standley 27914* (US), *Woodson et al. 1520* (A, MO). VERAGUAS: Isla Coiba, *Mendez 120* (US).

Pax and Hoffmann [Pflanzenreich **85** (IV, 147, XVI): 17, 1924] referred the Pittier collection from Taboga Island to var. *paniculata* Muell.-Arg. (DC., Prodr. **15**(2): 802, 1866), on the basis of the sparse indument and truncate leaf-bases. However, it remains to be demonstrated that the six varieties recognized by Pax and Hoffmann are geographically defined races, and there seems to be no need to apply any subspecific names to the Panamanian populations of *A. villosa*.

3. **Acalypha macrostachya** Jacquin, Hort. Schoenbr. **2:** 63, *t. 245*, 1797.

A. seemannii Kl. in Seemann, Bot. Voy. Herald 102, 1853.
A. macrostachya **α** *hirsutissima* (Willd.) Muell-Arg., Linnaea **34:** 11, 1865; DC., Prodr. **15**(2): 810, 1866.
A. macrostachya **β** *sidaefolia* (H.B.K.) Muell-Arg., loc. cit.
A. macrostachya **γ** *macrophylla* (H.B.K) Muell.-Arg. in Mart., Fl. Bras. **11**(2): 345, 1874.

Tree, or sometimes shrub, ca 3-8 m high; monoecious or dioecious; trunk ca 3-5 cm diam; stems nearly glabrous to densely tomentose. *Leaves* membranous; petioles glabrous to densely tomentose (2-)4-20 cm long; stipules broadly lanceolate to linear-lanceolate, acuminate, flat, sparsely to densely pubescent, 5-13 mm long; blades ovate to ovate-lanceolate, ca 10-20 cm long, 5-15 cm broad, glabrate to tomentose on both surfaces, 5-7-nerved at base, mostly with 6-10 veins on each side, the base barely to distinctly cordate, the margins crenate-serrate with ca 25-60 teeth on a side, the apex abruptly acuminate. *Inflorescences* axillary, spicate, normally unisexual; ♀ spikes becoming 15-30 cm long, loosely flowered, with ca 15-65 bracts, sometimes distinctly pedunculate; ♂ spikes ca 6-20(-40) cm long, densely flowered, 3-5 mm thick, sessile or short-pedunculate. *Pistillate flowers* solitary; bracts broader than long, ± reniform, 2.5-3.1 mm long, 4.4-5 mm broad, increasing and foliaceous in fruit to 5-8 mm long, with ca 11-20 shallow acute or acuminate lobes mostly 1.5-2.2 mm long, ± strigose-hirsute especially along the veins; calyx-lobes obscure; ovary densely hispid-tomentose, the styles free, strigose-hispid on the back, pinnatifid along their entire length into stoutish segments (the longer subequal to the style), mostly 3-4 mm long. *Capsules* 3.3-3.7 mm in diam, hispid, not glandular; seeds ellipsoidal, narrowed at one end, brownish-gray, smooth (minutely foveolate), ca 1.9-2 mm long, the caruncle an ill-defined whitish streak up to ca 1.5 mm long.

Common and widespread from southern Mexico to Peru, Bolivia, and Brazil.

BOCAS DEL TORO: Changuinola River, 10-15 mi S of mouth, *Lewis et al. 878* (MO); Changuinola Valley, Lincoln Creek, *Dunlap 432* (GH, NY); Chiriquí Lagoon, Water Valley, *von Wedel 1640* (GH, MO), *2158* (MO); Western Valley, *von Wedel 2701* (GH, MO). CANAL ZONE: Barro Colorado I, *Aviles 934* (F), *Shattuck 843* (F), *843b* (MO, US), *Standley 31353* (US), *Woodworth & Vestal 439* (A), *561* (A); Cerro Galero, *Stern & Chambers 31* (MO); Empire to Mandinga, *Piper 5470* (US), *5482* (US); Frijoles, *Allen 917* (MO), *Piper 5821* (US); Gamboa, *Bro. Heriberto 24* (US); 6 mi N of Gamboa, *Tyson 3487* (MO); Gatuncillo, *Piper 5625* (US); Las Cascadas Plantation, nr Summit, *Standley 29514* (US);

Madden Dam, *Dwyer & Robyns 15* (MO); vic of Río Cocolí, *Stern et al. 340* (DAV, MO); betw Río Grande & Pedro Vidal, *Pittier 2700* (GH, NY, US); 1 mi NW Summit, *Blum et al. 2349* (MO). COCLÉ: N of El Valle de Antón, *Allen 3687* (MO), *4219* (MO), *Allen & Alston 1848* (F, MO). COLÓN: vic of Giral, *Blum & Tyson 517A* (MO). DARIEN: vic of Garachiné, *Pittier 5521* (US); Paca, *Williams 751* (US); nr Río Canglon, *Duke & Bristan 357* (MO); Río Pirre, *Duke & Bristan 8274* (MO). HERRERA: Macaracas, Río La Villa, *Tyson et al. 3139* (MO). LOS SANTOS: Cerro Grande, Loma Prieta, *Lewis et al. 2229* (MO); Guayabo, W of Tonosí, *Stern et al. 1890* (MO); 10.8 mi S of Macaracas, *Lewis et al. 1619* (MO); 12 mi S of Macaracas, *Tyson et al. 3079* (MO). PANAMA: Juan Díaz, *Standley 30554* (US); Río Tapia, *Maxon & Harvey 6679* (US), *Standley 28230* (US).

4. **Acalypha leptopoda** Muell.-Arg., Linnaea **34:** 39, 1865; in DC., Prodr. **15**(2): 824, 1866; Pax & Hoffm., Pflanzenreich **85**(IV, 147, XVI): 174, 1924.

A. leptopoda β *glabrescens* Muell.-Arg. in DC., Prodr. **15**(2): 824, 1866.
A. lotsii J. D. Sm., Bot. Gaz. **20:** 544, 1895.

Shrub to 3 m high; monoecious; branches with spreading pubescence. *Leaves* membranous; petioles tomentulose, mostly 2-8 cm long; stipules linear-lanceolate, tip subulate, 7-17 mm long, glabrous; blades ovate to ovate-lanceolate, mostly 5-18 cm long, 2.5-9 cm broad, glabrate except for tufts of hairs in axils of veins beneath and with minute reddish glands (disappearing in age), 5-7 veined at base but pinnately veined above (with ca 5-7 additional lateral veins on each side above the basal ones), the base obtuse to rounded or subcordate, the margins rather coarsely serrate (teeth ca 25-40 on a side), the apex acuminate. *Inflorescences* axillary, spicate; ♀ spikes mostly 1-bracted (and then simulating solitary flowers), occasionally 2-bracted (rarely more), conspicuously stalked, the peduncle 10-20 mm long, lengthening to 40 mm in fruit; ♂ spikes at more proximal axils, ca 2-7 cm long, loosely flowered, ca 1.5 mm across, the peduncles 1-2 cm long. *Pistillate flowers* solitary, enveloped by subtending bract, sessile; bracts ca 3 × 6 mm at anthesis increasing to 4 × 9-10 mm in fruit, cut ca ½ way in 13-17 lanceolate acuminate lobes ca 1.5-2 mm long (lobes becoming ± deltoid in fruit), strigose-hispidulous; ovary densely hispidulous-tomentose, the styles free, erect, nearly glabrous, ca 4-5 mm long, divided in the distal ⅔ into 10-12 subulate-tipped segments. *Capsules* verruculose-hispidulous; seeds ellipsoidal, slightly beaked, grayish-brown, smooth, ca 1.5-1.7 mm long, the caruncle obscure.

Woods and thickets (often second-growth), 500-1800 m, southern Mexico to western Panama.

CHIRIQUÍ: Alto Lino, *Bro. Maurice 729* (MO, US); Bajo Mono, *Davison 464* (A, MO); vic of Boquete, *Lewis et al. 619* (DAV, F, GH, K, MO, NY, UC, US), *Maxon 5003* (NY, US), *Pittier 2916* (US), *Woodson & Schery 709* (GH, MO), *766* (GH, MO).

The Panamanian specimens of *A. leptopoda* are probably all referable to var. *glabrescens* Muell.-Arg., but it is doubtful if that name has much significance. Although *A. leptopoda* is a rather variable species, its races have never been carefully analyzed.

5. **Acalypha diversifolia** Jacquin, Hort. Schoenbr. **2:** 63, *t.* 244, 1797.

A. leptostachya H.B.K., Nov. Gen. Sp. Pl. **2:** 96, 1817.
A. panamensis Kl. in Seemann, Bot. Voy. Herald 101, 1853.
A. leptostachya γ carpinifolia Muell.-Arg., Linnaea **34:** 35, 1865.
A. diversifolia β leptostachya (H.B.K.) Muell.-Arg. in DC., Prodr. **15**(2): 854, 1866.
A. diversifolia γ carpinifolia (Muell.-Arg) Muell.-Arg., loc. cit.

Shrub 2-4 m high; monoecious; stems glabrous or sparsely pubescent. *Leaves* chartaceous; petioles 0.5-2 cm long; stipules lanceolate, subulate-acuminate, subindurate, distinctly convex at base, glabrate, (2.5-)4-8 mm long; blades elliptic to ovate- or obovate-lanceolate, (5-)8-15 cm long, (2-)2.5-6(-8) cm broad, ± glabrate except along the veins and minutely pustulate, pinnately veined (veins ca 5-7 on a side), the base narrowed, obtuse or subcordate, the margins crenate-serrate (teeth ca 20-40 on a side), the teeth sometimes callose, the apex abruptly acuminate. *Inflorescences* axillary, spicate; spikes sessile, bisexual, with 1 or 2 up to 6 ♀ bracts at the base, or entirely ♂; ♂ spikes (or parts of spikes) ca 3-8 cm long, loosely to densely flowered, 1.5-4 mm thick. *Pistillate flowers* sessile, 2-3 per bract; bracts ± ovate, ca 3-4.5 mm long and broad, shallowly 6-8-toothed (typically with 1 large central acute lobe and 2 or 3 much smaller lateral teeth), nearly or quite glabrous, foliaceous in fruit; ovary densely hispidulous-muriculate, the styles free, erect, slightly hispidulous at base, ca 1.5-2 mm long, divided in the distal half into a number of slender lobes. *Capsules* verruculose-hispidulous, 2.2-2.3 mm diam; seeds ellipsoidal, indistinctly beaked, grayish, nearly smooth (minutely foveolate), ca 1.2-1.5 mm long, the caruncle not well-defined.

Common in thickets or montane rain-forest, southern Mexico to Peru, Bolivia, and Brazil.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 114* (A, GH, NY, US), *1977* (GH), *Dunlap 236* (F, US); vic of Chiriquí Lagoon, *von Wedel 1041* (MO); id., Old Bank I, *von Wedel 1993* (GH, MO); id., Water Valley, *von Wedel 935* (GH, MO), *958* (GH, MO), *1587* (GH, MO). CANAL ZONE: Barro Colorado I, *Elmore X7* (GH, US), *Miller 2072* (MO), *Shattuck 22* (MO), *311* (F), 733 (F, MO, US), *842* (F, MO, US), *1141* (F), *Standley 40836* (US), *Woodworth & Vestal 325* (A, MO); Chagres, *Fendler 281* (GH, MO, US); Chiva-Chiva Trail, *Maxon & Harvey 6509* (US); Darien, *Macbride 2718* (F, MO, US), *Standley 31599* (US), *31618* (US); El Paraíso, *Pittier 2528* (US); Empire to Mandinga, *Piper 5458* (GH, US), *5516* (NY, US); Fort Randolph, *Standley 28713* (US); *29851* (US); Fort San Lorenzo, *Tyson & Blum 3684* (MO); Fort Sherman, *Standley 30954* (US), *31000* (US), *31105* (US); vic of Frijoles, *Allen 920* (MO), *Maxon 4702* (NY, US), *Piper 5781* (GH, US), *Standley 27561* (US); nr Frijoles, Río Agua Salud, *Piper 5864* (US); Galena Point, *Blum & Dwyer 2148* (MO), *2149* (MO); Gamboa, *Standley 28394* (US); betw Gatun and Fort Sherman, *Johnston 1729* (GH, MO); Gatun, *Hayes s.n.* (GH), *Bro. Heriberto 111* (GH, NY), *Standley 27289* (US); nr Gorgona, *Maxon 4743* (US); Juan Mina, *Piper 5693* (US); Las Cascadas Plantation, *Standley 25742* (US), *29595* (US), *29642* (US); Obispo, *Standley 31676* (US); Old Fort San Lorenzo, *Piper 5972* (US); Río Grande, nr Culebra, *Pittier 2528* (GH, NY, US); Río Indio de Gatun, *Pittier 2811* (GH, NY, US); Río Paraíso, *Standley 29888* (US); Río Providencia, 12 mi S of Colón, *Tyson & Blum 3943* (MO). CHIRIQUÍ: Peninsula de Burica, vic of San Bartolomé, *Woodson & Schery 920* (MO, NY). COCLÉ: El Valle de Antón, *Allen 1668* (MO), *Bro. Maurice 775* (US), *Miller 1824* (MO, US). DARIEN: vic of Caná, *Williams 954* (US); Cerro Piriaque, *Tyson et al. 3819* (MO); vic of Pinogana, *Pittier 6550* (US); betw Pinogana and Yavisa, *Allen 263* (MO). HERRERA: vic of Ocú, Río Pasoancho, *Stern et al. 1732* (MO). LOS SANTOS: Quebrada Bejuco, 16 m S of Macaracas, *Tyson et al. 2911* (MO); Quebrada Ocho Paso,

Stern et al. 1823 (MO); 11 mi N of Tonosí, *Tyson et al. 2983* (MO). PANAMA: Cermeño, *Dwyer & Robyns 94* (MO), *126* (MO); Cerro Campana, *Blum & Miller 2293* (MO); Río Tapia, *Standley 28229* (US), *30689* (US), VERAGUAS: Canazas, *Tyson 3629* (MO).

6. **Acalypha septemloba** Muell.-Arg., Flora **55:** 27, 1872.

? *Ricinocarpus irazuensis* O. Ktze., Rev. Gen. Pl. **2:** 616, 1891.
Acalypha irazuensis (O. Ktze.) Pax & Hoffm., Pflanzenreich **85** (IV, 147, XVI): 53, 1924.

Herb, evidently perennial from rhizome-like base; monoecious; to ca 0.5 m high; stems slender, spreading, with strigose or recurved hairs. *Leaves* membranous; petioles mostly 0.5-1.7 cm long; stipules lanceolate, acuminate, dark, pubescent, ca 1.5-2.2 mm long; blades ovate, ca 2-4 cm long, 1.5-2.8 cm broad, conspicuously strigose on both sides and with minute reddish glands beneath, 5-veined at base, the base truncate to rounded, the margins crenate-serrate (ca 10-25 teeth on a side), the apex acute. *Inflorescences* spicate; spikes unisexual, at distant nodes; ♀ spikes terminal, sessile or subsessile, cylindrical, densely flowered, ca 1-2 cm long, 3-4 mm broad; ♂ spikes axillary, ± sessile, densely flowered, 0.7-1.2 cm long, 2-2.5 mm thick. *Pistillate flowers* 2 per bract; bracts ± ovate, mostly with 7 gland-tipped obtuse lobes cut ca ½ way, becoming ca 3-3.5 mm broad; calyx-segments 3, elliptic, pointed, pubescent, ca 0.7-0.8 mm long; ovary densely hirsute-hispid and muriculate, the styles glabrous or nearly so, rather thick, ca 2.2-3.3 mm long, with 2-5 distal subulate branches. *Capsules* not seen; seeds [ex Muell.-Arg.] ovoid, minutely foveolate, ca 1 mm long.

Mountains, Costa Rica and western Panama.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, *White 67* (MO).

Kuntze's *R. irazuensis,* although described as having 3-5-lobed ♀ bracts, agrees so closely with *A. septemloba* in other respects that it is probably synonymous.

7. **Acalypha polystachya** Jacquin, Hort. Schoenbr. **2:** 64, *t. 246,* 1797; Pax & Hoffm., Pflanzenreich **85** (IV, 147, XVI): 42, 1924.

Herb to ca 1 m high; stems glabrate, with minute glandular droplets on young tips. *Leaves* membranous; petioles minutely puberulent, glabrate, 5-14 cm long; stipules linear-lanceolate, acuminate, glabrate, 11-13 mm long; blades ovate, ca 7-20 cm long, 4-12 cm broad, completely glabrate (hairs rare and scattered on veins), strongly 3-veined (and with 2 much weaker veins) at base, otherwise pinnately veined (ca 8 additional major veins on a side), the base rounded or truncate, the margin serrate (teeth 22-35 on a side), the apex acuminate. *Inflorescences* spicate, unisexual, ♀ spikes terminal and often in the upper axils as well, 6-11 cm long, loosely flowered, with ca 30-50 bracts, 1-1.5 cm across; ♂ spikes axillary, ca 1-2.5 cm long, with peduncles 5-20 mm long. *Pistillate flowers* paired, sessile; enveloping bracts glabrous 7-10.5 mm long (or smaller in depauperate plants), cut ca ½ way into 9-12 lanceolate, attenuate-acuminate lobes, the middle ones ca 5-6 mm long; calyx-lobes obscure; ovary minutely hispidulous, the styles free,

sparsely and obscurely hispidulous at base, distally laciniate into ca 6-10 subulate lobes 1.5-2.5 mm long. *Capsules* glabrous; seeds ovoid, beaked, prominently rugose, 2.5-2.8 mm long.

Weedy habitats, Mexico to Peru.

BOCAS DEL TORO: Chiriquicito, to 5 mi S along Río Guarumo, *Lewis et al. 2077* (BM, DAV, GH, MO, US). CHIRIQUÍ: 2 mi SW Guabala, *Tyson et al. 4248* (MO).

8. **Acalypha alopecuroidea** Jacquin, Coll. **3:** 196, 1790; Icon. Pl. Rar. 3: 19, *t. 620*, 1792; Pax & Hoffm., Pflanzenreich **85** (IV, 147, XVI): 22, 1924.

A. alopecuroidea var. *glandulifera* Kl. in Seemann, Bot. Voy. Herald 102, 1853.
A. alopecuroidea **β** *polycephala* b. *glanduligera* (Kl.) Muell.-Arg., Linnaea **34:** 50, 1865.

Herb, apparently annual; monoecious; stem and branches with appressed-incurved hairs intermixed with spreading ± gland-tipped hairs. *Leaves* membranaceous; petioles 1-3.5 cm long; stipules lanceolate, pubescent, 0.7-1.3 mm long; blades ovate, mostly 2-8 cm long, 1.5-5 cm broad, glabrate except for straight hairs on veins beneath, 5-veined at base, the base rounded to subcordate, the margins rather coarsely serrate (12-20 teeth per side), the apex abruptly short-acuminate. *Spikes* terminal and axillary; ♀ spikes terminal, short-pedunculate (peduncle ca 2-7 mm long), ellipsoidal to cylindrical, ca 1-4 cm long, 1-1.5 cm broad, sometimes with a terminal pedunculate ebracteate ♀ flower; ♂ spikes axillary, ± interrupted, ca 2-5 mm long, with peduncles 1-5 mm long. *Pistillate flowers* solitary, sessile; bracts densely hispid with sharp hairs ca 1-2 mm long and shorter mostly gland-tipped hairs, 4.5-7 mm long, with 3-5 lobes, the longer central lobes ca 3-5 mm long, deltoid with a green subulate tip mostly 2-4 mm long; ovary hispidulous and with glandular-capitate hairs, the styles unbranched, 2-7 mm long. *Capsules* glabrate; seeds ellipsoid or ovoid, smooth (minutely foveolate), grayish, 1-1.1 mm long, the caruncle inconspicuous, ca 0.3-0.4 mm long.

A widespread weed in the Caribbean area, from southern Louisiana and the Bahamas south to Panama, Colombia, and Venezuela.

CANAL ZONE: vic of Miraflores Lake, *Tyson 1391* (MO); Miraflores Locks, *Tyson 1259* (MO). COLÓN: vic of Sardinilla, 7-8 mi E of cement plant, *Blum & Tyson 490* (MO). DARIEN: El Real to Pinogana, *Stern et al. 285* (DAV, MO). PANAMA: sabanas N of Panama City, *Bro. Paul 519* (US); Panama Viejo, *Duke 5708* (MO); Taboga I, *Pittier 3555* (US), *Standley 27033* (US), *Woodson et al. 1515* (MO, NY).

9. **Acalypha arvensis** Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. **3:** 21, 1841.

Herb ca 2-5 dm high; stems moderately to densely pubescent with ± incurved, appressed hairs, gland-tipped hairs absent. *Leaves* membranaceous; petioles densely pubescent, mostly 1-2.5 cm long; stipules lanceolate, acuminate, pubescent, ca 1.5-2.5 mm long; blades ovate, mostly 3-6 cm long, 1.5-3 cm broad, strigose-hirsute above, glabrate beneath except on the veins, 5-veined at base, the base cuneate, the margins crenate-serrate (12-18 teeth on a side), the apex acute. *Spikes* all axillary; ♀ spikes with peduncles 6-12 mm long, ellipsoidal to short-cylindric,

ca (1-)1.5-2 cm long, 1-1.5 cm broad, usually with a terminal projection 4-7 mm long bearing 5-10 nodes of ♂ flowers (and occasionally a terminating ebracteate ♀ flower); ♂ spikes densely pubescent, uninterrupted, ca 5-20 mm long, with peduncles 3-25 mm long. *Pistillate flowers* solitary, sessile; bracts hispid with sharp hairs ca 0.5-1.5 mm long and slender gland-tipped hairs (ca 0.5-1 mm long), 4-8 mm long, with 5 lobes (plus occasionally 1 or 2 smaller extra lobes), the longer central lobes mostly (1.5-)2.5-5 mm long, deltoid with a green subulate tip 0.8-3 mm long; ovary apically 3-carinate, hispidulous, not glandular, the styles 1.7-4 mm long, with 3-5 distal branches. *Capsules* sharply carinate, hispid to hispidulous; seeds ellipsoidal, smooth (minutely foveolate), grayish, 1.2-1.3 mm long, the caruncle 0.4-0.6 mm long.

A widespread neotropical weed, from Mexico south to Peru, Bolivia, and Brazil.

BOCAS DEL TORO: Changuinola River, *Stork 6* (US), *127* (US); Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2135* (DAV, MO); Isla Colón, vic of Chiriquí Lagoon, *von Wedel 2821* (GH, MO, NY). CANAL ZONE: Ancon, *Piper 5818* (US); Balboa, *Standley 32115* (US); Fort San Lorenzo, *Burch et al. 1044* (DUKE, F, MO); Fort Sherman, *Tyson & Blum 3774* (MO); Frijoles, *Ebinger 630* (MO); Gamboa, *Bro. Heriberto 65* (US), *Pittier 4791* (US), *Standley 28358* (US); Gatun, *Hayes 237* (NY), *Piper 5997* (US), *Standley 27313* (US); Miraflores Lake, *White & White 195* (MO); betw Peluca Hydrographic Sta & Quebrada Peluca, *Steyermark & Allen 17237* (MO); Quarry Heights, *Dwyer 2602* (MO); Sosa Hill, *Standley 25241* (US). CHIRIQUÍ: vic of Boquete, *Davidson 634* (A, MO, US), *Lewis et al. 419* (DUKE, F, GH, K, MO, NY, UC, US), *Bro. Maurice 734* (US), *Pittier 2912* (NY, US), *Woodson & Schery 715* (MO); W slopes of Cerro Horqueta, *Allen 4830* (MO); vic of Puerto Armuelles, *Woodson & Schery 821* (GH, MO). DARIEN: El Real, *Duke 5039* (MO); El Real to Pinogana, *Duke 5129* (MO); vic of Yape, *Allen 865* (GH, MO). PANAMA: 5-6 mi E of Chepo, *Duke 4016* (DAV, MO); Corozal Rd, nr Panama, *Standley 26814* (US); Juan Díaz, nr Río Tapia, *Maxon & Harvey 6743* (US); San José I, *Johnston 900* (GH). VERAGUAS: 5 mi E of La Mesa, *Blum & Tyson 673* (MO).

Acalypha aristata H.B.K. was reported from Panama by Pax and Hoffmann [Pflanzenreich **85** (IV, 147, XVI): 23, 1924] on the basis of a specimen collected at Gamboa (*Pittier 4791*). However, that collection actually represents *A. arvensis*, and no specimens of *A. aristata* have been seen from Panama. Nevertheless, since the latter occurs in northern Colombia, it may eventually be detected here. Although vegetatively similar and probably closely related, it may be readily distinguished from *A. arvensis* by its terminal ♀ spikes and 2-flowered ♀ bracts.

25. DALECHAMPIA

Dalechampia L., Sp. Pl. 1054, 1753; Gen. Pl. ed. 5, 473, 1754.

Undershrubs or perennial herbs; mcnoecious; stems often scandent or twining, with irritating hairs. *Leaves* alternate, petiolate, stipulate, and usually with a pair of stipels at apex of petiole; blades simple to palmately lobed or divided. *Inflorescences* terminal on axillary short-shoots (or apparently axillary when side-shoots are contracted), bisexual, distinctly pedunculate, flowers subtended by conspicuous bilabiate involucre of 2 stipulate bracts; bracts simple to palmately lobed, often white or colored; flowers in contracted cymules; ♀ cymule proximal, 3-flowered, subtended by 2 or 3 bractlets; ♂ flowers in a pleiochasium of several 1-3-flowered

cymules, associated with a pulviniform nectary compounded from modified bractlets of suppressed ♂ cymules. *Staminate flowers* with articulated pedicels; calyx globose and entire in bud, splitting into 3-6 valvate segments at anthesis; disc and petals absent; stamens (5-)10-35(-90), the filaments connate into a stout column, the anthers dehiscing longitudinally; pollen grains oblong, coarsely ornamented with a massive reticulum; pistillode absent. *Pistillate flowers* pedicellate or subsessile; calyx-lobes 5-12, imbricate, usually ± lobed or pinnatifid, accrescent in fruit; disc and petals absent; ovary of 3 (rarely 4) carpels, the ovules 1 per locule, the styles connate into an elongated column, often dilated into a peltate compound stigma. *Fruits* capsular, of 3(-4) elastically dehiscent cocci, the endocarp crustaceous or woody, the columella persistent; seeds globose or ellipsoid, not carunculate, endosperm present, the cotyledons broad.

This taxonomically isolated genus of some 125 species cannot be confused with any other in Panama. The characteristic bilabiate involucre is often conspicuously colored, creamy white as in *D. scandens* and *D. tiliifolia* or pinkish as in *D. dioscoreifolia*, and seems to remain green at anthesis only in *D. cissifolia*. Observations of pollinators, which are nearly lacking for the entire genus, would be well worth the effort by investigators in Panama.

a. Leaves mostly lobed or compound (occasional ones, especially the smaller, may be unlobed).
  b. Leaves 3-5-lobed; involucral bracts ± creamy or white at anthesis.
    c. Involucral bracts 3-lobed, to the middle or deeper, 5-nerved, 1.5-3 cm long; leaves mostly 3-lobed ..... 1. *D. scandens*
    cc. Involucral bracts merely 3-dentate at apex, 7-9-nerved, 3-6.5 cm long; leaves dimorphic (trilobed and unlobed leaves on the same or separate branches ..... 2. *D. tiliifolia*
  bb. Leaves compound, leaflets usually 3(-4); involucral bracts green even at anthesis ..... 3. *D. cissifolia*
aa. Leaves always unlobed, ± ovate and cordate.
  d. Stigma conspicuously dilated, well over 1.5 mm broad; involucral bracts not trifid at the apex; peduncle (1-1.8 cm) much longer than the subtending axis (less than 1 cm) ..... 4. *D. dioscoreifolia*
  dd. Stigma very slightly dilated, less than 1.5 mm broad; involucral bracts shallowly trifid at apex; peduncle (1-2 cm) much shorter than the subtending axis (7.5 cm long or more) ..... 5. *D. friedrichsthalii*

1. **Dalechampia scandens** L., Sp. Pl. 1054, 1753, var. **scandens.**

Perennial vine (but often flowering the first year); stems woody and thickened at base, above twining and climbing, 1.5-5 mm thick or more; aerial stems subterete, somewhat channeled, green, ± hispid, the young tips densely hispid-puberulent. *Leaves* alternate; stipules becoming reflexed and brownish, ovate-lanceolate, acute, pubescent and ciliate abaxially, nearly glabrous adaxially (except near base), obscurely striate, (2-)3-5.5 mm long, 1.5-3 mm broad; petiole ± hispid as the stems, subterete, 2-12 cm long; stipels greenish, lanceolate, 1-3 mm long, glandular at base, ciliate and pubescent (especially abaxially); blades thinly to rather stiffly chartaceous, cordate at base, above greenish, rather sparsely pubescent, and somewhat rugose, beneath paler and more densely pubescent; usually deeply 3-lobed, sometimes 5-lobed, the lobes cut more than ½ way to the base,

rarely unlobed, usually with 5 main veins at base, mostly 3-10 cm long and 2.5-11 cm broad, the lateral lobes asymmetrically elliptic or ovate, abruptly acute or acuminate, the middle lobe elliptic-oblong or -obovate, abruptly narrowed to a short acuminate tip, 2-7 cm long, 1-5 cm broad, the veins conspicuously raised beneath, the tertiary veinlets tending to be scalariformly parallel. *Inflorescences* 1 or 2 on short axillary shoots (axis usually 5-10 mm long), subtended by reduced leaves; peduncles 2.5-5 cm long at anthesis, becoming 4-6 cm long in fruit. *Involucral bracts* 3-lobed ca halfway to the base, minutely glandular-toothed along the margin, generally 5-veined from the base, at anthesis distinctly whitish (lobe-tips sometimes remaining green), (1.5-)2.5-3 cm long and broad later turning green and becoming (2-)3-3.5 cm long and broad, pubescent with both crisped and stinging hairs (less densely to very sparsely so on the adaxial side); stipules reflexed, asymmetrically ovate- or oblong-lanceolate, greenish, ciliate-pubescent on both sides, ca 4-7.5 mm long. *Pistillate cymule* sessile, 3-flowered; adaxial bractlets 2 or coalesced into 1, ca 3-6 mm high, whitish, broader than high, sericeous on both sides, margins ciliate but not glandular, crystalliferous hairs sparse, the abaxial bractlet ca 4-6 mm high, oblong, somewhat greenish, similarly pubescent, crystalliferous hairs absent. *Staminate cymule* terminal, peduncle densely hirsutulous, 2.5-3.5 mm long; involucel 2-lipped, subglabrous, ca 2-4 mm high and 6-7.5 mm broad, with mostly 9 or 10 ♂ flowers in 3 cymules; ceriferous bractlets forming 2 laminate masses, the secretion copious and resinous. *Staminate flowers* with pedicels short and stout (1 mm long or less); buds ca 2 mm in diam, appearing glabrous (minutely hispidulous with crystalliferous hairs), splitting at anthesis into (3-)4 acute green lobes; stamens ca 25-35, the staminal column ca 1-1.3 mm long, the filament tips free, 0.1-0.2 mm long, the anthers deeply 4-sulcate, ca 0.4-0.6 mm long. *Pistillate flowers* subsessile at anthesis; calyx-lobes 8-12, unequal, deeply fimbriate lobed, the lobes ca 3-5 on a side, subulate, gland-tipped; ovary minutely hispidulous, oblate, the style cylindrical, 4-8 mm long, abruptly dilated distally into peltate stigma ca 0.8-1.3 mm across. *Central fruiting pedicel* up to ca 1.2 cm long, lateral pedicels shorter; fruiting calyx-lobes mostly 5-9 mm long, 0.4-0.8 mm broad, with conspicuously gland-tipped cilia, sharp-pointed hairs ca 1-1.5 mm long and minute crystalliferous hairs (less than 0.5 mm long). *Capsules* oblate, ± smooth (minutely hispidulous), ca 8.5-10 mm in diam, the cocci distinctly carinate, ca 5.5-7.5 mm long; seeds subglobose, smooth, with ricinoid brown-and-gray mottling, (3-)3.5-4(-4.6) mm across.

Widespread in tropical America, often in secondary shrubbery; reported from Africa but such reports still lack confirmation.

CANAL ZONE: Balboa, *Standley 32142* (US). COCLÉ: Aguadulce, *Pittier 4933* (NY, US). PANAMA: Corozal Rd, *Standley 26766* (US); Exposición, *Bro. Heriberto 278* (US); Las Sabanas, *Bro. Heriberto 196* (US), *Standley 25883* (US); Panama, *Bro. Paul 514* (US); San José I, *Johnston 396* (GH, MO), *839* (GH); Taboga I, *Woodson et al. 1549* (MO), *1550* (A, MO).

Although *D. scandens* is probably the most widespread species in the genus, it is surprisingly uncommon in Panama compared to *D. tiliifolia*. Pax & Hoffmann [Pflanzenreich **68** (IV, 147, XII): 34, 1919] refer the Coclé collection of Pittier

to var. *mollis* rather than to var. *scandens*. However, some of the other collections from Panama have involucral bracts smaller than 3 cm and it seems doubtful that this is a valid diagnostic character. Whatever subspecific taxa may be recognized in a monographic study of *D. scandens*, our Panamanian plants rather closely resemble the West Indian ones and thus will probably remain with the nominate variety.

2. **Dalechampia tiliifolia** Lam., Encycl. Méth. Bot. **2:** 257, 1786.—Fig. 18.

Clambering vine; stems twining, 2-4 mm thick, striate-ribbed, retrorsely incurved-pubescent. *Leaves* alternate; stipules 3-5 mm long, caducous; petiole pubescent as the stem, (1.5-)2.5-14 cm long; stipels lanceolate, 1-3.5 mm long, pubescent, more or less glandular at the base; blades polymorphic, of 3 kinds—(a) undivided blades: ovate, cordate and 5-veined at the base, (6-)10-16 cm long, (5-)7-11 cm broad; (b) blades with one lateral lobe (as in *Sassafras*); and (c) 3-lobed blades, lobed more deeply than ½ way to the base, 7-16 cm long, 8-17 cm broad, the middle lobe oblong to obovate, ± abruptly acute or acuminate, (4-)6-11 cm long, (2-)2.5-4(-6) cm broad; margins finely serrulate or subentire, the lamina densely pubescent to tomentose beneath, with a reticulum of conspicuously raised veins. *Inflorescences* 1 or sometimes 2 per short axillary shoot, the axis (3-)7-25 cm long; peduncles (1-)1.5-4 cm long at anthesis, becoming (1-)2.5-7 cm long in fruit, the involucral bracts broadly ovate, 3-toothed at the tip (middle tooth 3-7 mm long), generally 7-9-veined from the base, tomentose on both sides, distinctly whitish at anthesis, (2-)3.5-5(-6) cm long, becoming green in fruit, (3.5)4-6 cm long; stipules 2-4.5 mm long. *Pistillate cymule* with auriculate adaxial bractlet, subglabrous, the margins ciliate, 5.5-6.5 mm high, 10-11 mm broad; abaxial bractlet broadly ovate or obovate, 5-7 mm high, 8-11 mm broad. *Staminate cymule* with stout peduncle 3.5-5 mm long, sparingly to densely hirsutulous; involucel 2-lipped, subglabrous; lip facing bract entire, reniform, 2.5-3 mm high, 7-10 mm broad, the lip facing female cymule 3-parted, the lateral lobes broadly obovate, the center lobe oblong to obovate; ♂ flowers 9 or 10; ceriferous bractlets conspicuously fimbriate at the tips, secretion resinous and sticky. *Staminate flowers* with slender pedicels 4-8 mm long, articulated at about ⅔ height; mature buds ca 3-4 mm in diam; calyx-lobes (3-)4-6, 3.3-3.8 mm long; stamens (25-)30-45, the staminal column rather slender, 2.5-4 mm long, the free filaments densely hispidulous. *Pistillate flowers* with calyx-lobes 9-12, fimbriately lobed (ca 6-10 gland-tipped lobes on each side); ovary densely hispidulous, the style cylindrical, slender, 7-12 mm long, the stigma peltate-concave, 1.3-2.7 mm in diam. *Central fruiting pedicel* ca 1-1.8 cm long, laterals shorter; fruiting calyx-lobes mostly 8-13 mm long, 0.9-2 mm broad, with densely hispid subulate lobes. *Capsules* 9.5-10.3 mm in diam, densely hispid, the cocci 6.5-8.5 mm long; seeds somewhat compressed, elliptic in outline, (3.3-)3.7-4.8 mm long, ricinoid-mottled.

Widespread in tropical America from Honduras to Brazil, not attaining such high latitudes as *D. scandens*.

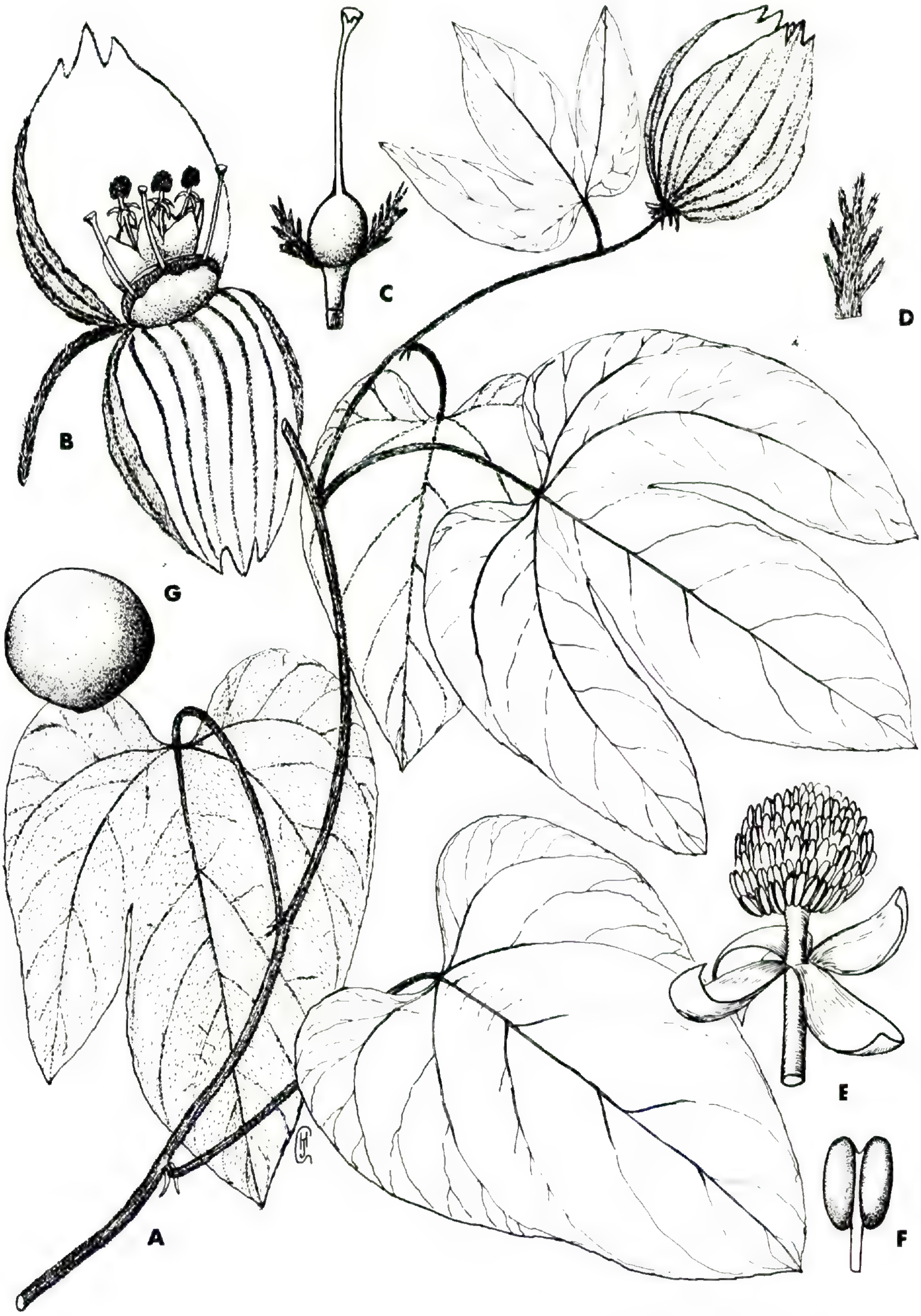

Fig. 18. *Dalechampia tiliifolia* Lam.: A, habit (ca ×½); B, inflorescence (ca ×1); C, ovary (ca ×2); D, female flower, calyx lobe (ca ×5); E, male flower (ca ×5); F, anther (ca ×10); G, seed (ca ×4). After *von Wedel 2154* (MO).

BOCAS DEL TORO: Changuinola Valley, *Dunlap 395* (F, GH); Water Valley, *von Wedel 1730* (GH, MO), *2154* (MO). CANAL ZONE: Ancon, *Bro. Celestine 61* (US), *Williams 42* (NY, US); Balboa, *Standley 25529* (US), *26093* (US); Balboa Heights, *Greenman & Greenman 5064* (MO); Barro Colorado I, *Brown 153* (F), *Wetmore & Abbe 156* (F, GH); Cerro Gordo, *Standley 26011* (US); Chagres, *Fendler 279* (GH, MO); Chiva-Chiva trail, *Piper 5716* (US); Colón to Empire, *Crawford 415* (NY); Culebra, *Pittier 2153* (US); Curund, *Harvey 5223* (F); Darien, *Macbride 2700* (F), *Standley 31648* (US); Empire to Mandinga, *Piper 5440* (US); Farfan Beach to Palo Seco, *Burch et al. 1411* (MO), *Hunter & Allen 443* (MO, NY); Fort Randolph, *Standley 28721* (US); Gamboa, *Standley 28491* (US); Gatun, *Standley 27305* (US); Miraflores, *White & White 46* (MO), *Blum 2060* (MO); Obispo, *Standley 31793* (US); Paraíso, *Hayes 165* (GH), *791* (NY); Punta Paitilla, *Piper 5420* (US); Summit, *Tyson 2783* (MO). CHIRIQUÍ: San Félix, *Pittier 5128* (US). COCLÉ: Bismarck, *Williams 278* (NY); rd to El Copé, *Burch et al. 1376* (MO). COLÓN: France Field to Cativa1, *Standley 30351* (US); Juan Minas plantation, *Allen 4132* (MO). DARIEN: Río Chico, *Burch et al. 1110* (MO). HERRERA: betw Las Minas & Pesé, *Burch et al. 1331* (MO), 10 mi S of Ocú, *Tyson et al. 2809* (MO). PANAMA: Bella Vista, *Piper 5344* (US); Capira to Potrero, *Dodge & Hunter 8647* (MO); Corozal Road, *Standley 26791* (US); Corozal to Pedro Miguel, *Cowell 397* (NY); San José I, *Johnston 1369* (GH, MO); Taboga I, *Macbride 2778* (F, US); Juan Díaz, *Standley 30602* (US); Panama, *Sargent 3* (US); Río Tapia, *Standley 28301* (US); Tumba Muerto Rd, *Standley 29790* (US). VERAGUAS: Soná, *Allen 1063* (MO).

3. **Dalechampia cissifolia** Poeppig in Poeppig & Endl. [Nov. Gen. Sp. Pl. **3:** 20, 1845] subsp. **panamensis** (Pax & Hoffm.) Webster, Ann. Missouri Bot. Gard. **54:** 193, 1967.

D. triphylla Lam. *α cissifolia* (Poeppig) Muell.-Arg. in DC., Prodr. **15**(2): 1239, 1866.
D. panamensis Pax & Hoffm., Pflanzenreich **68** (IV, 147, XII): 19, 1919.

Climbing vine; stems 1-2.5 mm thick, subterete, ± retrorsely pubescent. *Leaves* alternate; stipules reflexed, obliquely lanceolate, pubescent, 2.5-6 mm long; petiole pubescent, mostly 2.5-7.5 cm long; stipels lanceolate, 1.3-4.2 mm long; blades chartaceous, cordate at base, appearing glabrate on both sides except on veins, beneath paler and minutely hispidulous, 3-foliolate (rarely 5-foliolate), mostly 8-15 cm long, the margins undulate-dentate, the lateral lobes asymmetrically elliptic, the middle lobe narrowly elliptic-oblong to obovate, acute to acuminate, ca 6-14 cm long, 1-4 cm broad, petiolule 2-6 mm, the veins raised beneath but veinlets not conspicuously so. *Inflorescences* axillary and solitary to leaves on main stem (i.e. terminating reduced axillary branches less than 5 mm long); peduncle 1-2 cm long at anthesis, attaining up to 2.5 cm long in fruit. *Involucral bracts* 3-lobed ca halfway to base or sometimes nearly or quite unlobed, apparently greenish even at anthesis, with 5 main veins from the base, the margins ciliate and minutely dentate or subentire, 1.4-2.3 cm long, 1.3-2.5 cm broad, ca 1.5-2.5 × 1.6-2.9 cm in fruit, glabrous on both sides (but with minute stinging hairs on veins and some veinlets), the middle lobe of bract oblong, acute, 6-16 mm long, 3.3-7 mm broad, the stipules reflexed, 2.2-6 mm long. *Pistillate cymule* with 2 adaxial bractlets, discrete, obovate, subglabrous, the margins stiffly ciliate, ca 1.5-2 mm long, 1-1.5 mm broad; abaxial bract broadly oblong, ciliate-margined, ca 2.5-3.5 mm long. *Staminate cymule* with stout peduncle, very short (ca 1 mm long or less); involucre 2-lipped, subglabrous, 1.5-2 mm high, 5-8 mm broad, the lips reniform, entire; ♂ flowers 8 or 9; ceriferous bractlets truncate (not fimbriate), not

very resinous. *Staminate flowers* with pedicels ca 2-3 mm long, articulated at ca ¾ its length above the base, sparsely hispidulous; buds ca 1.5-2 mm in diam; calyx-lobes 4 or 5, reflexed; stamens 23-26, the staminal column stout, not over 1 mm long. *Pistillate flowers* with calyx-lobes 7-11, unequal, deeply pectinate-lobed (4-6 lobes on either side); ovary densely hispidulous, the style slender, clavate-thickened on one side above the middle, 5-6 mm long, the stigma concave, oblique, slightly expanded, ca 0.6-1 mm across. *Central fruiting pedicel* up to 1 cm long; fruiting calyx-lobes 5-9 mm long, 0.3-0.6 mm broad, lacinuli ca 0.5-1 mm long, bristly. *Capsules* minutely hispidulous, 6.6-8.5 mm in diam, the columella ca 2.5-3 mm long, the cocci 5-7 m long; seeds subglobose, (2.8-)3-3.7 mm long, ricinoid-mottled.

Tropical rain forest, Guatemala to Peru (and perhaps further south and east).

CANAL ZONE: Cerro Gordo, nr Culebra, *Pittier 2331* (lectotype US 676561; isotype NY); trail betw Gamboa and Cruces, *Pittier 3775* pro parte (F, US); woods nr Gatun, *Hayes s.n.* (GH), *7* (NY), *482* (NY, US); Las Cruces, *Pittier 3775* pro parte (GH, US); Miraflores, *White 123* (F, MO); Old Fort Lorenzo, mouth of Río Chagres, *Piper 5978* (US). COLÓN: France Field to Cativa1, *Standley 30275* (US). PANAMA: Camino de las Sabanas, *Bro. Heriberto 196* (US); Juan Díaz, *Standley 30485* (US).

A collection from Bocas del Toro (Chiriquicito, *Lewis et al. 2123*, MO), which unfortunately lacks flowers, resembles *D. cissifolia* in its trifoliolate leaves but differs in having hirsute stems and larger stipules (nearly 1 cm long). Discovery of flowering material will doubtless show it to be a species new to Panama and perhaps new to science.

4. **Dalechampia dioscoreifolia** Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. **3:** 20, 1845.

Climbing vine; stems 2-3 mm in diam, pubescent, subterete. *Leaves* alternate; stipules reflexed, lanceolate, long-acuminate, appressed-pubescent, ca 3-7 mm long; petiole pubescent with incurved hairs and sometimes with stinging hairs, mostly 2-5 cm long; stipels lanceolate, gland-tipped and usually glandular at base, 1.3-3.2 mm long; blades chartaceous, undivided, ovate with cordate base, usually 5-veined from the base, abruptly short-acuminate at the tip, mostly 7-15 cm long, 5-11 cm broad, pubescent on both sides but more or less glabrate in age, the margins crenately toothed to subentire, the veins distinctly raised on both sides but more conspicuously so beneath. *Inflorescences* axillary (i.e. terminating reduced axillary branches ca 3-7 mm long); peduncle 1-1.8 cm long at anthesis, becoming 1.8-2.3 cm long in fruit. *Involucral bracts* ovate-cordate, caudate-acuminate at the tip, 5-veined from the base, pink or white with darker red or purple veins, the margins lacerate-toothed (ca 10 teeth on each side), pubescent on both sides, distinctly petiolate; blades mostly (2.5-)3.2-3.8 cm long; petiole ca 8-10 mm long; stipules reflexed, the two pairs unequal, larger stipules ca 8-10 mm long, 5-8 mm broad. *Pistillate cymule* with adaxial bractlets absent, abaxial bractlet concave, glabrous, ca 5-5.5 mm long, the margins ciliate (not glandular). *Staminate cymule* with peduncle up to 1.5 mm long or sometimes scarcely evident;

involucel glabrous, of 4 distinct, broadly imbricate, chartaceous to subcoriaceous concave bracts; ♂ flowers 8 or 9; ceriferous bractlets fimbriate. *Staminate flowers* with pedicels ca 3.5-6 mm long, articulate near the top, glabrous below the articulation, hispidulous above; calyx-lobes 4, appressed-hispidulous without; stamens ca 20-30, the staminal column slender, 2.5-3.5 mm long, glabrous. *Pistillate flowers* with sepals 6-11, deeply pectinate-lobed, pubescent; ovary densely hispidulous, the style columnar, appressed-hispidulous, 3-5.5 mm long, the stigma peltate-disciform, ca 2-3.5 mm across. *Central fruiting pedicel* 1.9-2.5 cm long; fruiting sepals mostly 8-10 mm long, deeply dissected into rigid acuminate lanceolate lobes 2-5 mm long, lobes densely armed with stinging hairs. *Capsules* deeply 3-lobed, ca 12 mm in diam, the columella ca 5 mm long; seeds turgid, more or less cubical, asymmetrically crested, with low transverse ribbing, dark-mottled, 4.7-5.5 mm long.

Lowland rain forest, Costa Rica to Peru.

BOCAS DEL TORO: Almirante, *Blum 1325* (MO); Bocas del Toro, *von Wedel 239* (MO), *263* (MO), *365* (MO); Chiriquí Lagoon, *von Wedel 1114* (MO), *1263* (MO), *1381* (MO); Water Valley, *von Wedel 599* (MO), *1489* (MO), *1764* (MO), *1780A* (MO), *1818* (MO). CANAL ZONE: Barro Colorado I, *Shattuck 618* (F, US), *Wetmore & Abbe 11* (A, F, GH), *11A* (A); Las Cascadas Plantation, nr Summit, *Standley 25724* (US). COLÓN: France Field to Cativa1, *Standley 30232* (US), *30318* (US), *30356* (US). PANAMA: Cerro Azul, *Duke 9334* (MO); Chepo, *Duke 4075* (DAV, MO); El Llano to Río Mamoní, *Duke 5593* (MO); Río Tocumen, *Standley 26758* (US).

5. **Dalechampia friedrichsthalii** Muell.-Arg., Flora **55:** 45, 1872; Pax & Hoffm., Pflanzenreich **68** (IV, 147, XII): 52, 1919.

Climbing vine; stems ca 2-2.5 mm thick, terete, minutely pubescent and also sparsely hirsute. *Leaves* alternate; stipules reflexed, lanceolate, acuminate, striate, minutely pubescent and ciliate, 8-12 mm long; petiole pubescent as the stem, 5.5-9.5 cm long; stipels lanceolate, pubescent, glandular at base, 1.8-3 mm long; blades chartaceous, ovate, abruptly short-acuminate, deeply cordate at base (basal lobes overlapping), sometimes with a prominent tooth 3-5 mm long on one side, sparsely hirsute above, closely and minutely puberulous beneath, 7-14 cm long, 5-10 cm broad, the margins subentire (finely and inconspicuously dentate), the veins and veinlets very prominently raised beneath. *Inflorescences* axillary and solitary to leaves on the main stem, the involucre terminating a peduncle-like branch 7.5-10 cm long; leaf at base of peduncle with caducous blade, represented only by stipules; true peduncle only 1-2 cm long, hirsute above. *Involucral bracts* evidently pale at anthesis, ovate, shallowly 3-lobed at the tip, the middle lobe cuspidate-acuminate, ca 8-9 mm long, the blade becoming ca 3 cm long, margins lacerate, minutely pubescent and also hispid (especially on veins and lobes), 5-veined at the base and contracted into a thick petiole ca 1.5-2 mm long; stipules subequal, pubescent and hispid-ciliate, 12-13 mm long, 3.5-5 mm broad. *Pistillate cymule* with 2 adaxial bractlets, discrete, asymmetrically obovate, obscurely toothed, 5-5.5 mm long, the margins hispid-ciliate but not glandular; abaxial bractlet broadly ovate-reniform, ca 4.5 mm long, over 6 mm broad, crenate-toothed, pubescent as the adaxial bractlets. *Staminate cymule* with peduncle stout, min-

utely pubescent, ca 1.5-2 mm long; involucel of 4 distinct, broadly imbricate, firmly chartaceous concave bracts, each ca 4-5 mm high and 7-8 mm broad; ♂ flowers ca 10; ceriferous bractlets conspicuously fimbriate distally. *Staminate flowers* with pedicels 2-3 mm long, hispidulous, articulate near the top; buds ca 1.5-2.5 mm in diam; sepals 4 or 5; stamens (18-)25-33, the staminal column 1.3-2 mm long, hispidulous. *Pistillate flowers* with sepals 5-8, ovate-oblong, lacerate-fimbriate (but rachis broader than lobes), densely pubescent, 1.7-2.2 mm long at anthesis; ovary deeply 3-lobed, minutely short-hispidulous, the style slender, antrorsely minutely hispidulous below, 9.5-10 mm long, slightly dilated distally into a concave stigma 1-1.2 mm across. *Capsules* with cocci (ex Pax & Hoffmann) 8 mm long; seeds ca 4 mm across, slightly rugulose, mottled.

Known only from two collections, one in Costa Rica, incorrectly cited as Guatemala by Mueller, the other the Panamanian collection cited below.

COLÓN: Río Fató, *Pittier* 3866 (GH, NY, US).

This evidently rare species also belongs in sect. *Dioscoreifolieae* and is obviously related to *D. dioscoreifolia*, but not closely so. The much longer hypopodium, more short-petiolate involucral bracts, and longer styles with smaller stigmas clearly set *D. friedrichsthalii* apart.

26. PERA

Pera Mutis, Vet.-Akad., Stockholm, Nya Handl. **5:** 299, *t.* 8, 1784.

Trees; dioecious or rarely monoecious. *Leaves* alternate, simple, petiolate; stipules small or obsolete. *Inflorescences* axillary consisting of small clusters of stalked globose involucres each enclosing 3-10 sessile flowers; involucres 1-2 bracteolate at base, opening laterally at anthesis or valvate or, in one species, almost lacking. *Staminate flowers* 3-10, not all fully formed; calyx gamosepalous with 3 acuminate lobes; stamens 2-5, the filaments short and free or longer and basally connate, the anthers dorsifixed near base and longitudinally dehiscent; pollen grains prolate, tectate, 3-colporate. *Pistillate flowers* 2-5; naked; ovary 3-carpellate each with a single ovule, the 3 short styles connate basally. *Fruit* capsular, somewhat woody, dehiscence valvate; seeds ovoid or obovoid, compressed, smooth, shiny, carunculate.

A tropical American genus of about 25 species, two of which are reported from Panama.

a. Involucre well developed, enclosing flower buds before anthesis .....1. *P. arborea*
aa. Involucre absent or represented by a minute scale .....2. *P. aperta*

1. **Pera arborea** Mutis, Vet.-Akad., Stockholm, Nya Handl. **5:** 299, *t.* 8, 1784.—Fig. 19.

Tree to 20 m, glabrous or strongly lepidote and glabrate; dioecious. *Leaves* somewhat coriaceous; petioles to 2 cm long, deeply channeled to obscurely winged; stipules obsolete; blade elliptic to obovate, 6-12 cm long, 3-5.5 cm wide, the base

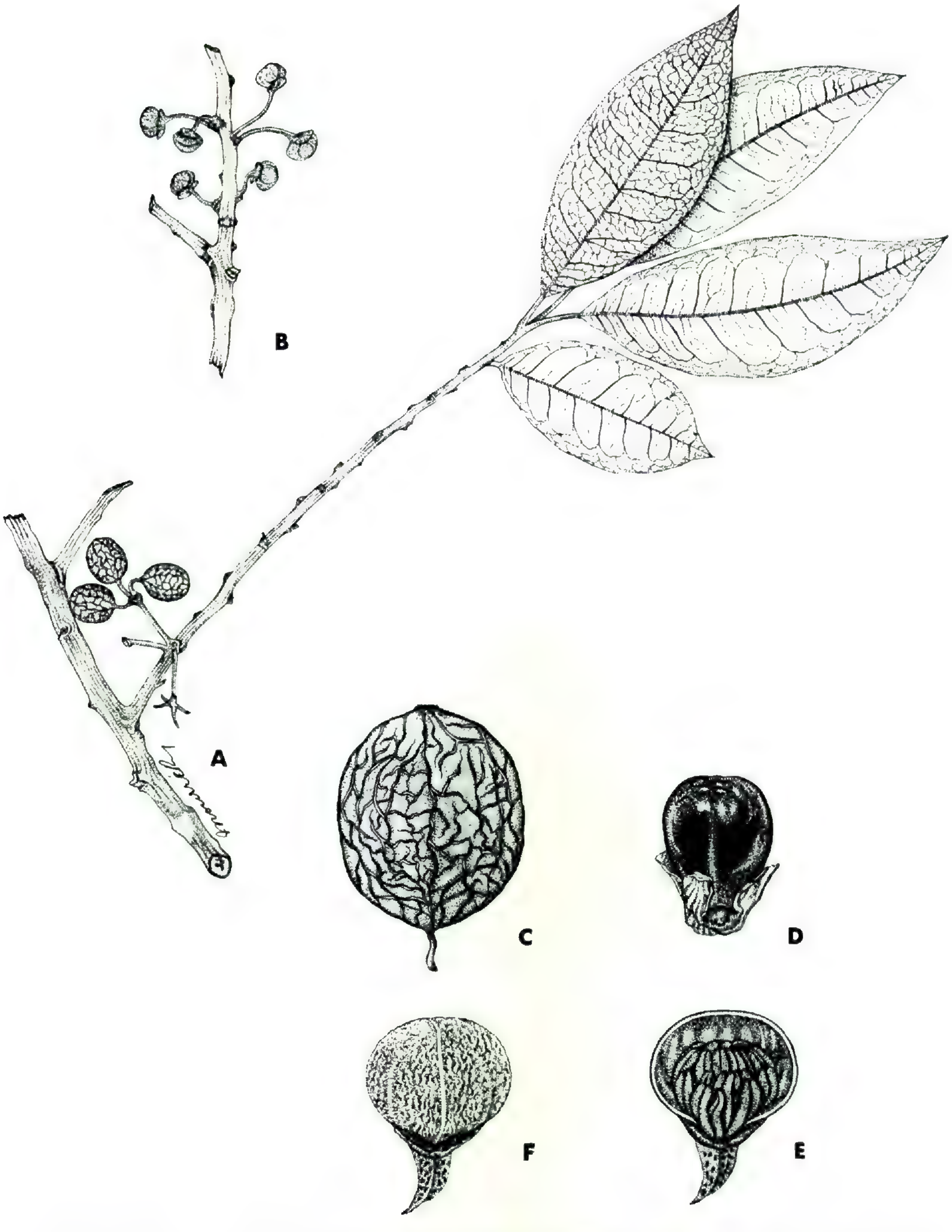

Fig. 19. *Pera arborea* Mutis: A, habit, fruiting branch (×½); B, branch with flower buds (×2); C, fruit (×2½); D, seed (×3); E, involucre cut away to show male flower (×8); F, unopened involucre containing male flowers (×8). A, C, D after *Tyson & Blum 4058* (MO); B, E, F after *Johnston 478* (MO).

rounded to acute, the margin entire, the apex bluntly to sharply acuminate. *Staminate flowers* 5-10 in each involucre, the bracteoles unequal with the larger ca 1 mm long, the involucre 3 mm diam, dehiscence lateral; calyx to 1.5 mm long, strongly toothed; stamens 4-6. *Pistillate flowers* usually 3 per involucre, the peduncle rarely more than 6 mm long before anthesis, the bracteoles and involucre resembling ♂. *Capsule* ellipsoid to obovate, ca 12 mm long, on stalk to 4 mm long, the surface coarsely ruminate with rather sharp edged wrinkles; seed obovoid, somewhat compressed, ca 5 mm long, black, shiny, the caruncle obvious.

British Honduras, Panama and Colombia. The tree is not particularly conspicuous and may be more frequent in moist forests than the rather small number of collections would suggest.

CANAL ZONE: Fort Sherman Reservation, *Maxon & Valentine 6975* (NY, US). COCLÉ: vic of El Valle de Antón, *Allen 775* (F, MO). COLÓN: nr Fato, *Pittier 4096* (F, NY, US), *4250* (US). DARIEN: forests nr Pinogana, *Pittier 6574* (US). PANAMA: Cerro Azul, *Dwyer s.n.* (MO), *Tyson & Blum 4058* (MO); Río Tapía, *Standley 30674* (K, US); San José I, *Johnston 15* (GH, MO), 233 (GH, MO), *411* (GH, MO), *447* (GH), *478* (GH, MO).

2. **Pera aperta** Croizat, Ann. Missouri Bot. Gard. **29:** 353, 1942.

Tree to 6 m, young shoots crustate-lepidote. *Leaves* somewhat coriaceous; petioles to 2 cm long; stipules obsolete; blade oblong, ca 5 cm long, 2-4 cm wide, the base rounded to cuneate, the margin subentire, somewhat revolute, the apex shortly acuminate. *Staminate flowers* not seen. *Pistillate flowers* 2-5, the peduncle slender, ca 1 cm long, the bracteoles ca 2 mm long, no involucre or the merest trace present. *Fruit* not seen.

COCLÉ: hills S of El Valle de Antón, *Allen 2506* (holotype US; isotype MO).

The overall appearance of the type specimen of this species is very close to that of *P. arborea*, but the absence or extreme reduction of the involucre is a clear distinguishing feature. The peduncle is also longer than that of the buds of most collections of *P. arborea* examined. Few other collections of this genus from areas similar to the type locality of *P. aperta* have been seen, and in their absence Croizat's judgement that this is more than an aberrant individual must be accepted.

Known only from the type collection.

27. SEBASTIANIA

Sebastiania Spreng., Neue Entd. Pflanzenk. **2:** 118, *pl.* 3, 1821.

Shrubs trees or herbs; monoecious or dioecious. *Leaves* alternate (rarely opposite), simple, petiolate; stipules small; blade serrulate or entire. *Inflorescences* spicate, terminal or opposite the leaves (or rarely axillary), usually bisexual. *Staminate flowers* in clusters of 2-3 or solitary at distal nodes, subtending bracts biglandular; calyx 3-lobed; petals and disc absent; stamens 3 or 2, the filaments free or basally connate and anthers extrorse; pollen grains subglobose, tectate, 3-colporate. *Pistillate flowers* solitary or rarely in small groups at base of spike,

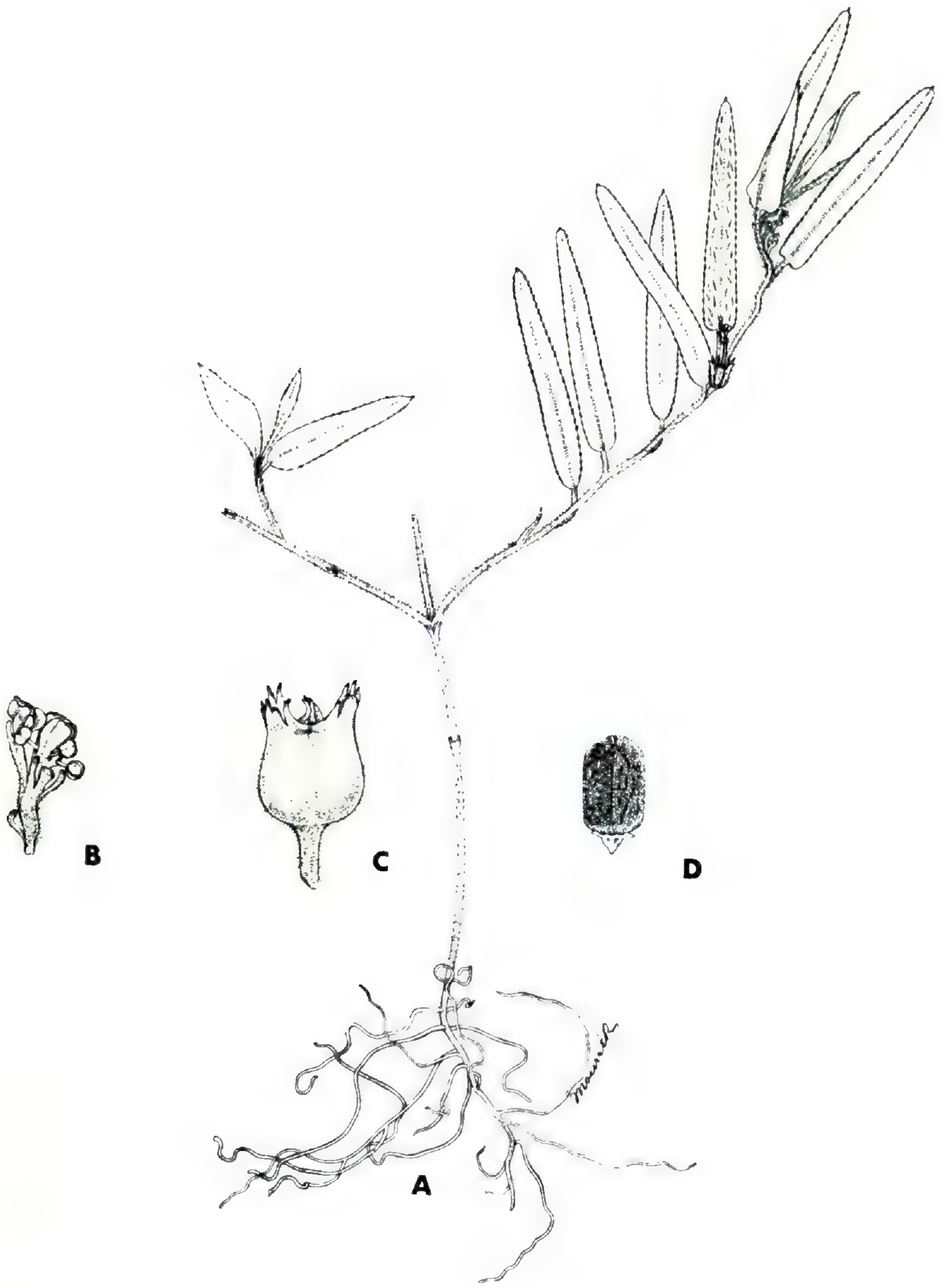

Fig. 20. *Sebastiania corniculata* (Vahl) Muell.-Arg.: A, habit (×1); B, male flower spike (ca ×8); C, fruit (×3); D, seed (×3). After *Allen 824* (MO).

subtending bracts biglandular; calyx 3-lobed; petals and disc absent; carpels 3 (rarely 2), the styles simple, connate at base or free, the ovules 1 per locule. *Fruit* capsular, smooth or armed; seed subglobose to cylindric, minutely carunculate, smooth.

About 90 species, three in the Old World tropics, most of the remainder in Brazil. The single representative in Panama is a small annual which has little superficial resemblance to the majority of species in the genus.

1. **Sebastiania corniculata** (Vahl) Muell.-Arg. in DC., Prodr. **15**(2): 1168, 1866.—Fig. 20.

Tragia corniculata Vahl, Eclog. Amer. **2**: 55, *pl. 19*, 1798.

Herb, annual; monoecious; stem sparsely branched, slender, ascending to 50 cm, hirsute or glabrate. *Leaves* alternate, membranous; petioles to 2 mm long; stipules minute; blade linear-lanceolate 16-32 mm long, 3-5 mm wide, hirsute or glabrous, the base obtuse to rounded, somewhat inequilateral, the margin serrate, sometimes obscurely so, the apex acute, often acuminate. *Inflorescences* bisexual with a female flower at the base of a male spike or unisexual with the solitary female flowers interaxillary. *Staminate flowers* in 10-12 flowered spikes 3-7 mm long borne opposite the leaves, the subtending bracts toothed, ca ¼ mm long, the pedicels ca ½ mm long; calyx-lobes broadly obovate ca ½ mm long; stamens 3, free. *Pistillate flowers* solitary, the pedicel ca ½ mm long; calyx-lobes elliptic, dentate, less than 1 mm long; ovary glabrous or sparsely hirtellous with 6 horn-like processes distally, the styles shortly connate. *Capsule* truncate-globose, ca 3.5 mm diam, the distal processes ca 1 mm long with additional flaps of tissue of a similar size developing on the sides of some fruits, the persistent columella ca 3 mm long, broadening from a slender base; seeds subcylindric, to 2.5 mm long, minutely pitted, the caruncle stipitate.

An inconspicuous member of the flora of the savannas and grassland of cut-over areas.

COCLÉ: Nata, *Allen 824* (F, MO). PANAMA: nr Las Sabanas, *Standley 40782* (US); along drowned Río Azote Caballo, *Dodge et al. 16840* (MO).

28. MABEA

Mabea Aublet, Hist. Pl. Gui. Fr. 867, *t.* 334, 1775.

Shrubs or trees with milky latex; monoecious. *Leaves* alternate, simple, petiolate; stipules usually obsolete; blade expanded, entire or toothed. *Inflorescence* racemose or paniculate, terminal, usually bisexual. *Staminate flowers* numerous, usually ternate in groups of 2-5 at upper nodes with each group subtended by a conspicuously biglandular bract; calyx small of 3-5 broad lobes; petals and disc absent; stamens numerous or rarely 2-3, the anthers almost sessile on a convex receptacle, extrorse; pollen grains somewhat prolate, tectate, 3-colporate. *Pistillate flowers* few, solitary (rarely 2-4 on branched peduncle) at basal nodes, subtending bract glandular to varying degrees; sepals 3-6, unequal, acute; petals and disc absent; carpels 3, each with 1 ovule, the styles connate in a long colum, free and simple above. *Fruit* capsular, endocarp hard, the columella persistent after dehiscence; seed carunculate, smooth or somewhat warty.

About 40 species, all in tropical America and with no more than three or four as far north as Central America. As treated here, the Panamanian specimens fall into two taxa, one of which shows a wide range of variation.

a. Leaves elliptic to lanceolate, usually 3-5 times as long as wide, the apex subacuminate; stamens 15-25 per ♂ flower ..... 1. *M. montana*

aa. Leaves broadly elliptic to ovate-elliptic, usually less than 3 times as long as wide, apex strongly long-acuminate; more than 30 stamens per ♂ flower ..... 2. *M. occidentalis*

1. **Mabea montana** Muell.-Arg. in DC., Prodr. **15**(2): 1151, 1866.—Fig. 21 (A-C).

Shrub or small tree. *Leaves* membranous; blade 7-12 × 1.5-3 cm, elliptic to lanceolate, the upper surface sometimes shiny, the base rounded, the margin serrate (sometimes obscurely so), the apex somewhat acuminate and often mucronate. *Inflorescence* a raceme of groups of ♂ flowers, ♀ usually solitary. *Staminate flowers* in groups of 3-5, the subtending biglandular bract at or near the base of the peduncle; calyx gamosepalous, the broad lobes fused for most of their length; stamens 15-25. *Pistillate flowers* 2-5, solitary at basal nodes, a single ♂ flower sometimes sharing the node, subtending bract eglandular; sepals 6, 3 much larger than the others. *Capsule* ovoid, to 16 mm long; seed ovoid, to 10 cm long, somewhat laterally compressed, dark brown, smooth.

Reported from Venezuela and Colombia, and in Panama most common in the lowland forests around the Canal Zone.

CANAL ZONE: vic of Ancon, *Piper 6022* (US), *6034* (US); Ancon Hill, *Killip 39954* (US), *Piper 5550* (US), *5570* (US), *5583* (US), *Standley 25156* (US), *26364* (K); low hill N of Balboa, *Gillespie P-30* (F); Balboa heights, *Greenman & Greenman 5074* (MO); Corozal *Standley 27634* (US); beach area Fort Kobbe, *Duke 4227* (MO); Howard Air Force Base, SE of Kobbe beach, *Oliver & MacBryde 1881* (GH, MO); woods nr Panama, *Hayes 715* (K). COCLÉ: Penonomé *Williams 53* (NY). DARIEN: Río Cucunati at Puente Quemado, *Duke 8816* (MO). PANAMA: Taboga I, *Macbride 2831* (F, US), *Miller 1841* (US), *Pittier 3586* (US).

2. **Mabea occidentalis** Bentham, Hooker's London Jour. Bot. **6:** 364, 1854.—Fig. 21(D).

Shrub or small tree. *Leaves* membranous to subchartaceous; blade 8-15 × 3-5 cm, broadly elliptic to ovate-elliptic, the upper surface usually shiny, the base obtuse to rounded, the margin subentire to bluntly serrate and often undulate, the apex strongly long-acuminate. *Inflorescence* a raceme of groups of ♂ and solitary ♀ flowers. *Staminate flowers* in groups of 3, the subtending biglandular bract at or near the base of the peduncle; calyx gamosepalous, the broad lobes fused for ca ½ length; stamens 30-45. *Pistillate flowers* 3-7, solitary at basal nodes, subtending bract eglandular or obscurely glandular; sepals 6, acute, subequal. *Capsule* ovoid, 11-17 cm long; seed ovoid, ca 8 mm long, slightly laterally compressed, smooth or obscurely warted.

Central America and northern South America to Brazil. Most of the collections seen from Panama have come from the Province of Panama or the Canal Zone, and the plant is most common in rather wet forests.

CANAL ZONE: Balboa *Standley 29302* (US); Barro Colorado I, *Brown 2* (F), *7* (F), *8* (F), *9* (F), *14* (F), *169* (F), *Frost 56* (F), *Killip 40025* (US), *Shattuck 253* (A, F), *Standley 31448* (US), *41033* (US), *Wetmore & Abbe 29* (A, F, GH) *Woodworth & Vestal 369* (A, F), *Wilson 54* (F); nr Fort Randolph, *Standley 28662* (US); *29852* (US); Galena Point, *Blum & Dwyer 2147* (MO); nr Gatun, *Hayes s.n.* (F, GH, K, MO, NY, US); Gatun Station, *Hayes 52* (NY), *118* (GH, US), *461* (NY); betw Gatun & Lion Hill, *Pittier 2565* (US); Matachin, *Cowell 196* (NY), *200* (NY); vic of Miraflores Lake, *White 188* (MO); Obispo, *Standley 31698* (US); Quebrada Ancha, *Steyermark & Allen 17106* (MO); Quebrada La Palma, *Dodge & Allen 17348* (F, K, NY, US); Río Chagres, 1 mi above Madden Lake, *Duke 4456* (MO); Río Paraíso, above East Paraíso, *Standley 29899* (US);

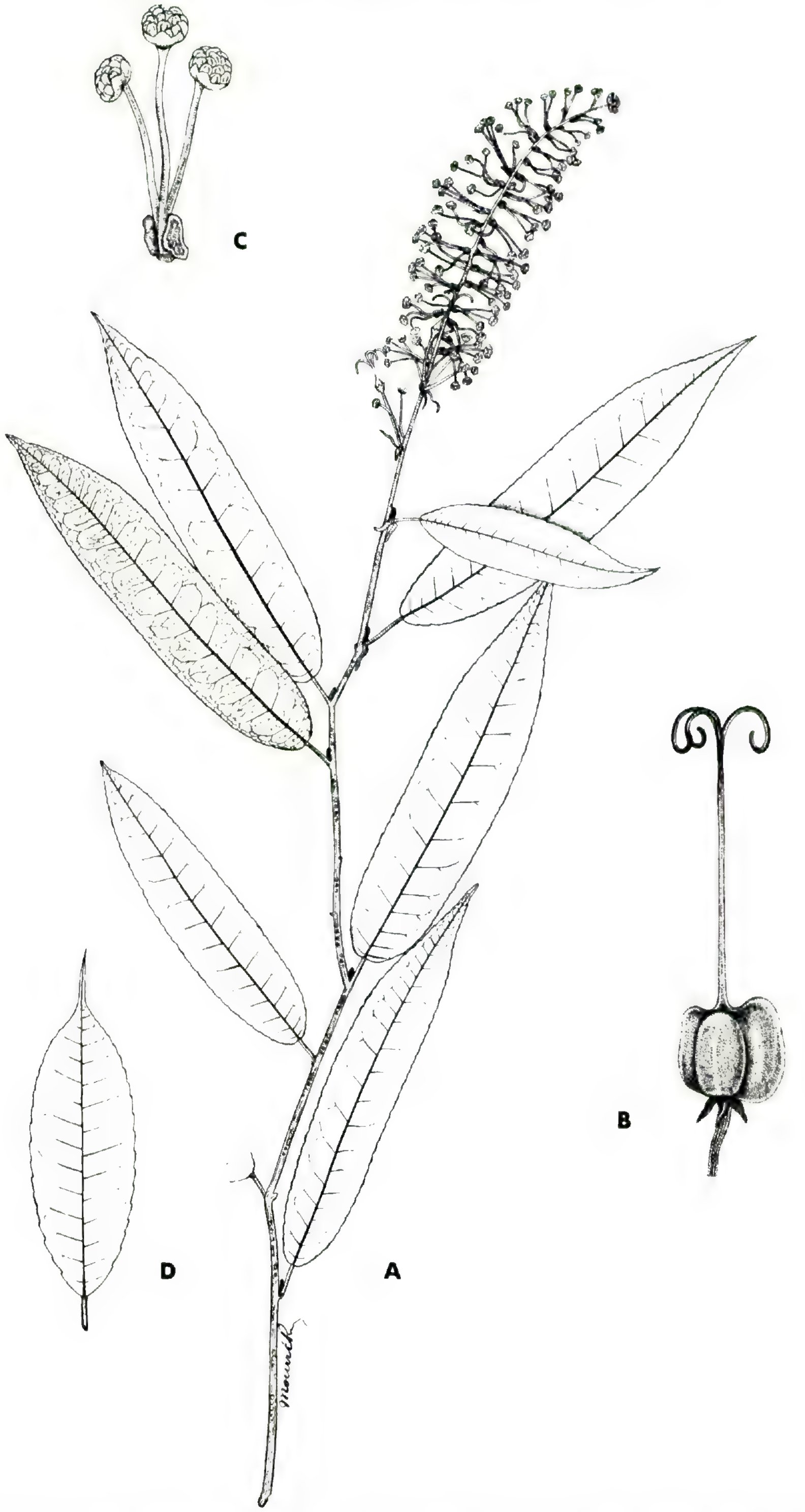

Fig. 21. *Mabea montana* Muell.-Arg.: A, habit (×½); B, young fruit (×4); C, male flower cluster (×4). A, C after *Standley 25156* (US); B after *Piper 6022* (US). *M. occidentalis* Bentham: D, leaf (×½). After *Johnston 1137* (MO).

s. loc., *Lee 1* (F, MO). COLÓN: summit of Cerro Santa Rita, *Allen 5102* (F, MO); Juan Mina plantation, Río Chagres above Gamboa, *Allen 4142* (F, MO). DARIEN: vic of La Palma, *Pittier 5502* (US); Río Sambu, 0-5 mi above Río Venado, *Duke 9260* (MO); San José River, *Duke & Bristan 405* (MO); ca 2 mi N of Santa Fé, *Duke 10249* (J. A. Duke pers. herb.). PANAMA: Cerro Jefe, *Dwyer & Gauger 7364* (MO), *Tyson 3399* (MO), *Tyson et al. 3209* (MO), *3351* (MO), *4355* (MO), *4366* (MO); upper Mamoni River, *Pittier 4486* (US); vic of El Llano, *Duke 5846* (MO); Río La Maestra, *Allen 21* (F, MO); Río Tapia, *Standley 28135* (US); Río Tocumen, *Standley 26728* (US); San José I, *Erlanson 162* (GH, US), *Johnston 408* (GH, MO), *1137* (GH, MO), *1053* (GH); Taboga I, *Standley 28003* (US). SAN BLAS: inland from airport at Mandinga, *Duke 8906* (MO). VERAGUAS: rd betw San Francisco & Santa Fé, *Stern et al. 33725* (MO, US).

The specimens from Panama show a great deal of variation but could not be assigned with any degree of satisfaction to the varieties cited by Pax [Pflanzenreich **52**(IV, 147, V):33, 1912] in his treatment of the whole genus. One collection from the E slope of Cerro Jefe (*Tyson et al. 3351*) and *Allen 5102* from 1200-1500 ft in Colón were particularly sturdy specimens, but apart from this overall larger size no differences were found from other collections. Several collections appeared to differ in the size of the female calyx, but no other distinguishing features were found. It seems possible that additional field work and study of complete specimens would allow some division of this taxon.

29. STILLINGIA

Stillingia Garden ex L., Mant. Pl. 19, 1767.

Perennial herbs, shrubs or small trees, glabrous throughout; monoecious. *Leaves* alternate, opposite or verticillate, simple, petiolate; usually with glandular filiform stipules and often with 2-3 cyathiform or scutelliform glands at the base of the blade. *Inflorescence* terminal, spicate, bisexual. *Staminate flowers* at distal nodes, solitary or in compressed cymules, subtending bracts biglandular; calyx 2-lobed; apetalous; disc absent; stamens 2, the filaments connate at base, the anthers extrorse; pollen grains ellipsoid to spheroid, usually 3-colpate. *Pistillate flowers* solitary at proximal nodes; sepals 3, usually distinct; petals absent; carpels 3 or 2, each with 1 ovule, the styles connate at base, simple. *Fruit* capsular, a hardened gynobase persisting after dehiscence; seed carunculate or not, rugulose or smooth, the endosperm mealy.

A genus of 25-30 species of the tropics and subtropics. All are from the New World except three in Madagascar and one in Fiji, but only one has been reported from Panama and this is known from only two collections.

Useful Reference:

Rodgers, D. J., A revision of *Stillingia* in the new World. Ann. Missouri Bot. Gard. **38:** 207-259, 1951.

1. **Stillingia zelayensis** (H.B.K.) Muell.-Arg., Linnaea **32:** 87, 1863.

Sapium zelayensis H.B.K., Nov. Gen. Sp. Pl. **2:** 65, 1817 (n.b. the pagination here and in subsequent citations of this work is from the quarto edition).

Shrubs or subherbaceous from a woody rootstock, spreading or erect to 1.5 m. *Leaves* membranous, alternate or subverticillate; petiole to 5 mm long; stipules

obsolete; blade elliptic, 3-5.5 cm long, 1-2.2 cm wide, the base acute with 2 cyathiform glands, the margin serrulate, the apex acute. *Inflorescence* to 7 cm long. *Staminate flowers* sessile in 3-5-flowered cymules, subtending bracts elliptic; calyx ca 1 mm long. *Pistillate flowers* sessile; sepals narrowly elliptic, ca 3 mm long; styles ca 3 mm long. *Capsules* obovoid, shallowly 3-lobed, to 1.8 cm diam, the lobes of gynobase 3-9 mm long; seed subspherical, ca 6 mm diam, smooth, shiny, the caruncle small.

CHIRIQUÍ: Boquete, savannas alt 4000 ft, *Davidson 750* (A, F, P, MO, US); Boquete, *Seemann s.n.* (K).

30. SAPIUM

Sapium P. Browne, Civ. Nat. Hist. Jamaica 338, 1756.

Excoecaria Muell.-Arg. in DC., Prodr. **15**(2): 1201, 1866 (pro parte).

Trees or shrubs, glabrous; monoecious or rarely dioecious; milky latex in stems. *Leaves* alternate, simple, petiolate, usually with two glands near apex; stipules small. *Inflorescences* spicate, terminal, bisexual. *Staminate flowers* in several-flowered clusters at distal nodes, subtending bract biglandular; calyx gamosepalous, 2-3-lobed; corolla and disc absent; stamens 2 or 3, the filaments free or connate at base, the anthers extrorse; pollen grains subglobose, tectate, 3-colporate. *Pistillate flowers* solitary at proximal nodes, subtending bracts usually biglandular; calyx gamosepalous (2-)3-5-lobed, sometimes obscurely so; corolla and disc absent; carpels 3 (rarely 2), each with a single ovule, the 3 styles simple, usually connate at least at base, the stylar column often early-deciduous. *Fruit* capsular, sometimes fleshy or somewhat woody, the columella usually persistent; seeds rounded, outer seed-coat fleshy, ecarunculate.

A genus of about 100 species, pantropical but with the majority from the New World.

The genus has the reputation of being difficult taxonomically, and this seems well justified with the incomplete specimens available in most herbaria. Dr. E. Jablonski of the New York Botanical Garden is working actively in the group, and it is unfortunate that this treatment must appear before he has published further. Separation of taxa and assignment of names is made here with some trepidation, particularly since the ranges that he gives for South American species (Phytologia **14:** 441-449, 1967) already cast some doubt on the correctness of some of my decisions.

a. Spikes in clusters of 3-5 (rarely fewer); ♂ flowers 2-5 at each node .....1. *S. aucuparium*
aa. Spikes solitary; ♂ flowers usually more than 5 at each node.
  b. Petiole without glands or with only vestiges near junction with blade; leaf-apices ± plane .....2. *S. eglandulosum*
  bb. Petiole with 2 prominent glands near junction with blade; leaf-apices ± cucullate.
    c. Leaves somewhat coriaceous, elliptic to obovate; styles fused only at base, strongly reflexed .....3. *S. caudatum*
    cc. Leaves membranous, elliptic-lanceolate; styles fused for much of length, not reflexed .....4. *S. biglandulosum*

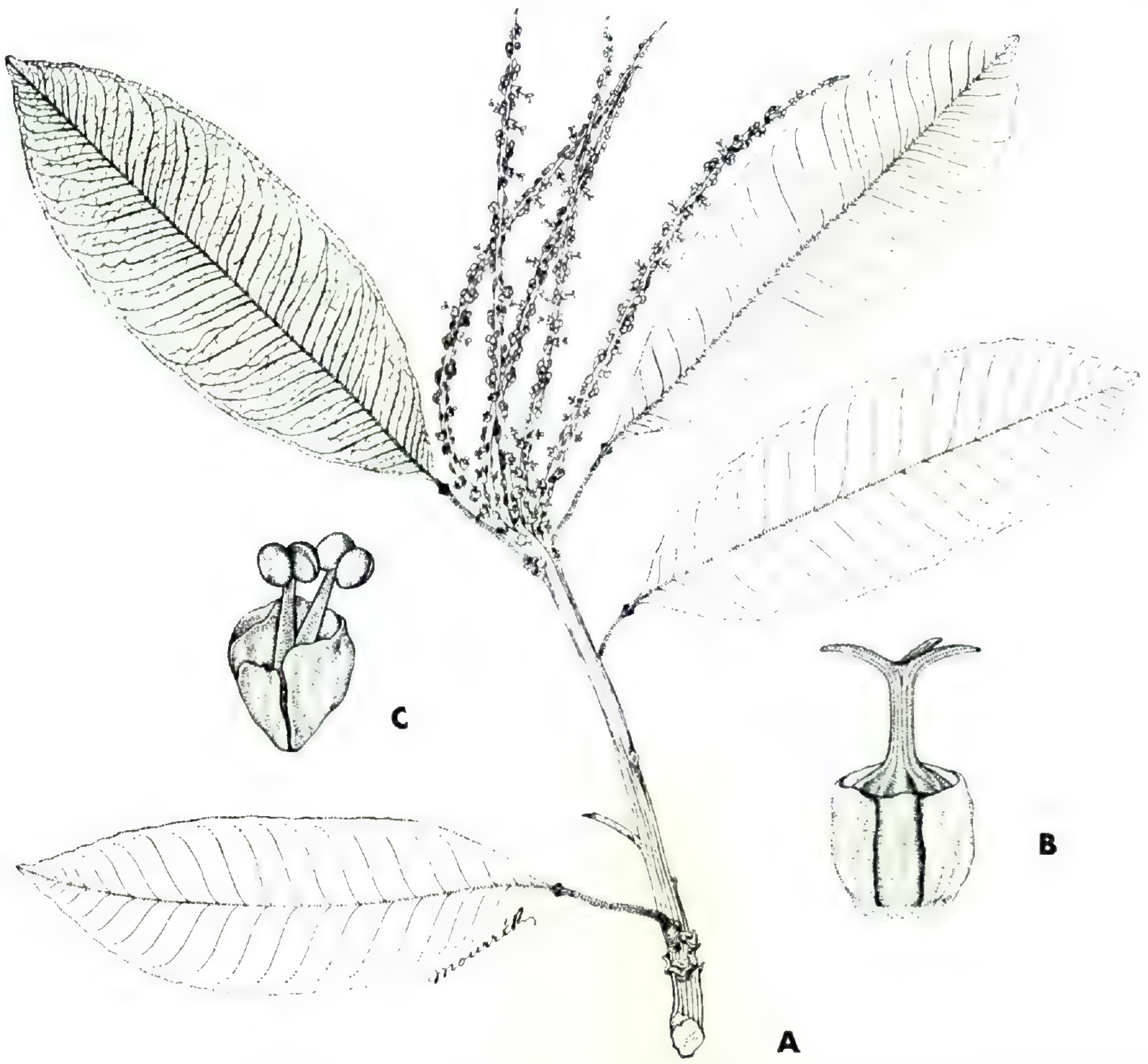

Fig. 22. *Sapium aucuparium* Jacquin: A, habit (×½); B, female flower (×8); C, male flower (×8). After *Dunlap 210* (US).

1. **Sapium aucuparium** Jacquin, Enum. Pl. Carib. 31, 1760.—Fig. 22.

S. jamaicense Sw., Adn. Bot. 62, 1829.
S. pleiostachys Schum. & Pittier, Contr. U.S. Nat. Herb. **12:** 164, *pl. 10*, 1908.
S. anadenum Schum. & Pittier, loc. cit., *pl. 11*.

Tree to 20 m; monoecious. *Leaves* membranous; petiole 2-3 cm long with the two glands at or near the apex, subopposite or alternate, stipitate to obsolete; stipules obsolete; blade elliptic to obovate, 9-12 × 3-5 cm, often rather glossy on both surfaces, the secondary veins many, parallel for most of their length, leaving midrib ± at right angles, the base obtuse, sometimes unequal, the margin subentire to regularly strongly tufted, the apex acuminate, sometimes cucullate. *Spikes* in clusters of 3-5 (rarely fewer), to 10 cm long, bisexual. *Staminate flowers* in groups of 2-3 (-5), the subtending bract prominent in young spikes, deltoid, to 3 mm long, caducous, the basal glands persistent, prominent; calyx minute to ca 1 mm long, 2-lipped; often caducous; stamens 2. *Pistillate flowers* 8-15, singly at the basal nodes of the spike, the bract equaling ♂, caducous but basal glands persistent, smaller than in ♂; calyx cupular of two unequal segments, free almost to base;

ovary orbicular, the styles simple, to 2 mm long, connate for ca ½ length, erect, upper half uncinate, the whole stylar column caducous leaving a short rounded peg. *Capsule* ovoid, to 8 mm long; seed flattened-ovoid.

Cuba, Jamaica, Central and northern South America. Quite widely distributed in Panama with no clear altitude or environmental preference.

BOCAS DEL TORO: region of Almirante, *Cooper 350* (F, US); Changuinola valley, *Dunlap 210* (US). CANAL ZONE: Barro Colorado I, *Kenoyer 661* (US). CHIRIQUÍ: Boquete, *Davidson 852* (F, MO, US); Progreso, *Cooper & Slater 197* (F, NY, US). SAN BLAS: Puerto Obaldia, *Pittier 4328* (US).

The application of this name and of *S. biglandulosum* (L.) Muell.-Arg. follows that of Croizat (Jour. Arnold Arb. **24:** 174 et seq., 1943).

2. **Sapium eglandulosum** Ule, Bot. Jahrb. **35:** 673, *f. 2A*, 1905.

Shrub or small tree (in Panama); monoecious. *Leaves* membranous; petiole 2-3 cm long, eglandular or with vestiges at base of blade; stipules obtuse, to 3 mm long, somewhat sheathing in young stems; blade obovate-elliptic, 13-18 × 5-7 cm, glabrous, the base acute, the margins entire or obscurely serrate, the apex long-acuminate, plane. *Spikes* solitary, to 7 cm long, bisexual. *Staminate flowers* in groups of 5-7, the bracts short, broad, to ½ mm long, the basal glands prominent, cupular, persistent; calyx cupular, ca 1 mm long, 2-lipped; stamens 2. *Pistillate flowers* 3-5, singly at the basal nodes, the bract short, as in ♂, prominently biglandular, the glands cupular; calyx cupular, 3-lobed; ovary orbicular, the styles simple, to 3 mm long, fused for half length, the upper half reflexed. *Capsule* not seen.

Brazil, Peru and Colombia. The two Panamanian collections represent an entirely credible extension of the range from that shown by Jablonski (op. cit.).

DARIEN: ascent of Cerro Pirro from Río Pirre S of El Real, *Duke 5334* (MO); Cerro Pirre, *Duke & Elias 13665* (MO, NY).

3. **Sapium caudatum** Pittier, Contr. U.S. Nat. Herb. **20:** 127, 1918.

Tree to 10 m; monoecious. *Leaves* somewhat coriaceous; petiole 1.5-4.5 cm long, the 2 stipitate glands at or near apex; stipules ovate, to 1 mm long or obsolete; blade elliptic to obovate (8-)13-17 × 2.5-5 cm, upper surface usually dull, the base obtuse, the margin irregularly toothed to subentire, the apex somewhat attenuate, usually strongly cucullate. *Spikes* solitary, bisexual. *Staminate flowers* in groups of 7-10, bract short and broad, ca ½ mm long, biglandular, the glands small; calyx ca ½ mm long, cupular, scarcely lobed; the stamens 2. *Pistillate flowers* 5-10, solitary at basal nodes, the bract as in ♂, caducous leaving two prominent glands larger than in ♂; ovary orbicular, styles simple, ca 2 mm long fused only at base and remainder of length reflexed to lie on surface of ovary, deciduous leaving a rounded peg. *Capsule* ovoid, somewhat stipitate, to 8 mm long; seed ovoid, flattened laterally, surface warted.

Range doubtful; the species was described from Panama.

CANAL ZONE: Barro Colorado I, *Oppenheimer 1513* (MO); Frijoles, *Hayes 709* (K); Gamboa, *Pittier 2603* (NY, US), *3713* (US, n.v.), *4058* (US); W of Limon Bay, *Johnston 5175* (MO). CHIRIQUÍ: S slope of Cerro Horqueta, *Pittier 3165* (US); vic of Concepción, *Allen 3475* (MO, NY). DARIEN: Uruti River, *Duke & Bristan 232* (MO). PANAMA: nr Chepo, *Klug 7* (US); vic of El Llano, *Duke 5838* (MO).

The syntypes cited for this name (*Pittier 2603, 3713, 4058*) were collected from a single tree at different seasons and show a remarkable diversity of leaf characters. The rest of the specimens from Panama are a good match for one or other sheet. It seems unlikely that a plant that ranges so widely in Panama should be restricted to that country, and it is probable that Dr. Jablonski will have other thoughts on the validity of this name. The Panamanian specimens have resemblances to Schumann & Pittier's *S. oligoneurum* and *S. thelocarpum* of Costa Rica and with the widely ranging *S. hippomane* G. F. W. Meyer, and may well prove not to be distinct.

Pittier described another species from Panama, *S. giganteum* (Contr. U.S. Nat. Herb. **20:** 128, 1918). No authentic material of this has been seen, but from the description it falls within the range of variation of *S. caudatum* as used here.

4. **Sapium biglandulosum** (L.) Muell.-Arg., Linnaea **32:** 116, 1863.

Hippomane biglandulosum L., Sp. Pl. ed 2, 1431, 1763.
Sapium aucuparium Jacquin, Select. Amer. Hist. 249, 1763, non Jacquin (Enum. Pl. Carib. 31, 1760).
S. salicifolium H.B.K., Nov. Gen. Sp. Pl. **2:** 52, 1817.
S. moritzianum Kl. in Seemann, Bot. Voy. Herald 100, 1853.
S. aucuparium Jacquin subsp. *moritzianum* (Kl.) Pittier, Contr. U.S. Nat. Herb. **20:** 128, 1918.
Stillingia haematantha Standley, Ann. Missouri Bot. Gard. **27:** 314, 1940.

Tree to 10 m; monoecious. *Leaves* membranous; petiole ca 1 mm long, the 2 apical glands prominent; stipules to 1 mm long, ovate; blade elliptic-lanceolate, 8-11 × 1.5-2 cm, glabrous, the base acute, the margin coarsely and evenly serrate, inrolled on drying, the apex somewhat attenuate and cucullate. *Spikes* solitary at apex of short laterals, to 8 cm long, bisexual or all ♂. *Staminate flowers* in groups of 7-10, the subtending bract lingulate, to ½ mm long, biglandular, the glands sometimes obsolete; calyx ca 1 mm long, 2-3 lipped; stamens 2. *Pistillate flowers* 1-8, singly at basal nodes, rather distant, the bract deltoid, fimbriate, biglandular; calyx cupular, 2-lobed; ovary orbicular, styles simple, fused for most of length and slightly expanded at apex, soon deciduous leaving a rounded peg. *Capsule* broadly ovoid, to 1 cm long, smooth; seeds broadly ovoid flattened laterally, the surface warty.

Panama and northern South America, perhaps to Brazil. A number of the Panamanian collections are from areas near the sea, but the species does not appear restricted to one altitude or habitat.

CANAL ZONE: upper Chilibre River, 1 mi below Chilibre, *Seibert 1514* (MO, NY, US); Culebra I, *Hayes s.n.* (GH); Fort Amador, *Tyson 2026* (MO); Las Sabanas, *Bro. Celestine 109* (US), *Pittier 6681* (US). COCLÉ: Aguadulce, *Pittier 4951* (NY, US); N rim El Valle de Antón, *Allen 1915* (type coll. of *Stillingia haematantha* GH, MO); vic of Las Uvas, *Allen 2575* (A, F). LOS SANTOS: Pediasi, *Dwyer 2495* (MO). PANAMA: Bella Vista,

Killip 12037 (US); vic of Juan Franco race track, nr Panama, *Standley 27778* (US); Sabana de Dormisolo, nr Chepo, *Pittier 4659* (US); Peña Prieta, nr Panama City, *Pittier 4070* (NY, US); Pedro Gonzales, Perlas I, *Allen 2583* (A, F).

One more group of specimens remains without a name. All have elliptic leaves 20-35 × 5-9 cm with an obtuse to rounded base, coarsely and evenly serrate margin and attenuate apex which may be somewhat cucullate. The veins are arcuate, prominent below, and the petiole has a pair of stipitate glands a little below the junction with the blade. The stipules are deltoid, to 2 mm long. All the shoots have a succulent appearance which suggests that they may be sucker growth or water shoots, and those of the sheets which include collection notes describe the plant as a shrub. None include any flowering or fruiting material. They do not unequivocably match any American material in the herbarium of the Missouri Botanical Garden, and will not be included in this treatment in the hope that later, more complete collections will enable someone to make good the omission.

31. HIPPOMANE

Hippomane L., Sp. Pl. 1191, 1753; Gen. Pl. ed. 5, 499, 1754.

Trees or shrubs with milky latex, glabrous; monoecious. *Leaves* alternate, simple, petiolate, with a single gland at junction with blade; stipules caducous; blade ovate-cordate, the base rounded, the margins bluntly serrate, the apex acute to short acuminate. *Inflorescences* terminal, spicate, bisexual. *Staminate flowers* clustered in several-flowered glomerules at the distal nodes, subtending bracts biglandular at base; calyx 2-3-lobed; apetalous; disc absent; stamens 2, the filaments connate, the anthers extrorse; pollen grains sub-globose, tectate, 3-colporate. *Pistillate flowers* solitary at proximal nodes; calyx 3-parted; apetalous; disc absent; carpels 6-9, the styles simple, connate at base, spreading above, the ovary smooth with one ovule per locule. *Fruit* drupaceous, apple-like, red or yellow; seeds ovoid, compressed, ecarunculate.

A genus of two or three species, one widespread in the Caribbean area, the others endemic to Hispaniola.

1. **Hippomane mancinella** L., Sp. Pl. 1191, 1753.—Fig. 23.

Tree to 10 m, much branched forming a rounded crown, the bark gray or red, often lichen covered. *Leaves* on slender petioles 3-5 cm long; blades ovate to elliptic, 5-10 cm long, 4-6 cm wide just below middle, somewhat shiny above with veins slightly raised particularly on drying, the base rounded to subcordate, the margin crenulate with 8-12 shallow teeth, the apex short-acuminate. *Inflorescences* to 10 cm long, stout, 1-2 ♀ flowers at base. *Staminate* calyx ca 1 mm long, the lobes broadly ovate. *Pistillate* calyx ca 3 mm long, ovate and somewhat acuminate. *Fruit* globose, to 3.5 cm diam, smooth; seed dark, ca 6 mm long.

Widespread and locally common near the upper edge of beaches from Florida and the Bahamas through Central America and the Antilles to Colombia and Venezuela.

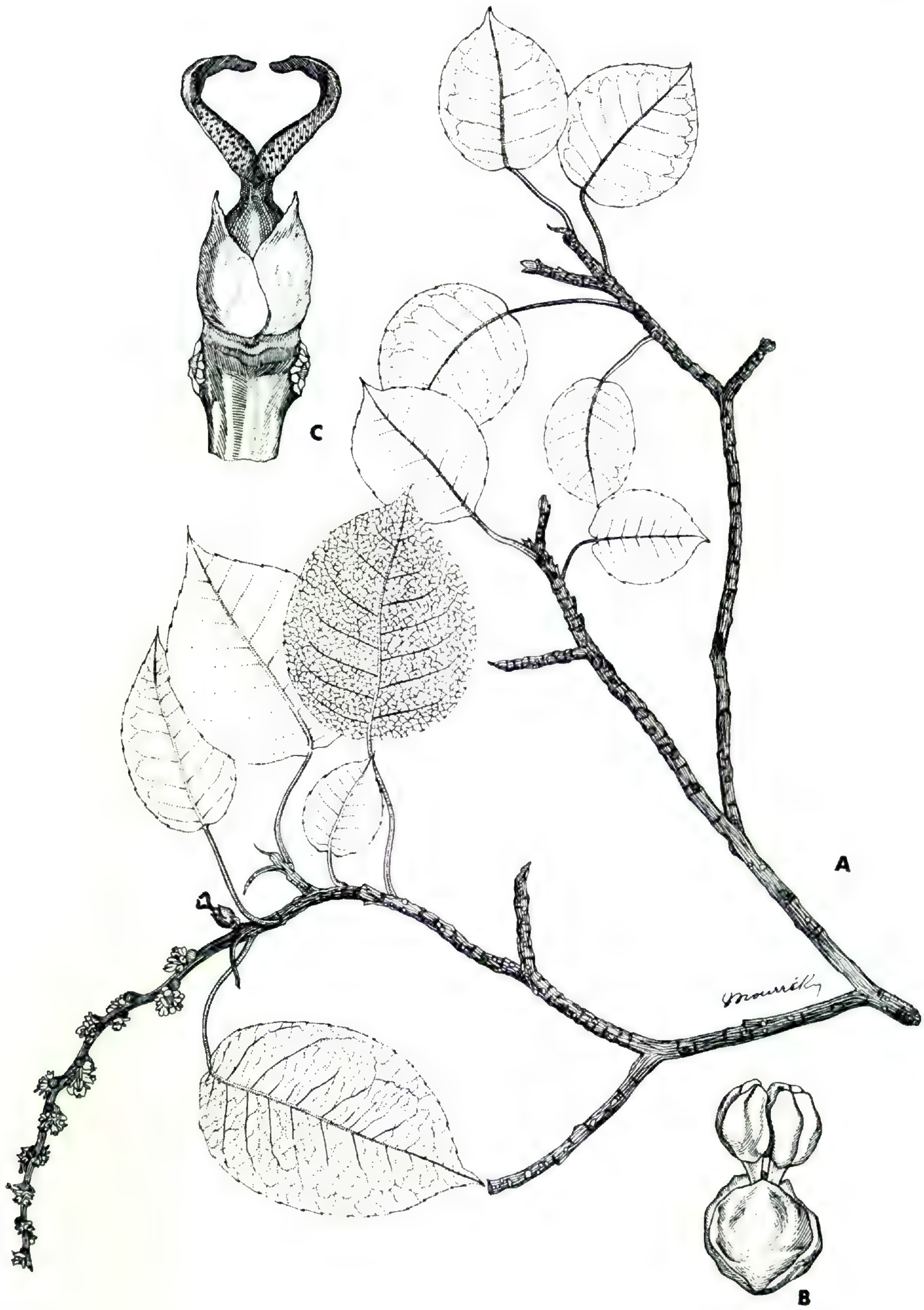

Fig. 23. *Hippomane mancinella* L.: A, habit (×⅔); B, male flower (×10); C, female flower (×10). A-B after *Christopherson 173* (US); C after *Standley 30777* (US).

CANAL ZONE: beach at Fort Kobbe, *Duke 4249* (MO). CHIRIQUÍ: vic of San Bartolome, Peninsula de Burica, *Woodson & Schery 935* (F, MO). COCLÉ: Santa Clara, *Burch et al. 1388* (GH, K, MO, NY, UC, US), *Ebinger 1128* (MO, US). DARIEN: Patino, *Pittier 5699* (US). PANAMA: vic of Nueva Gorgona, *Allen 2555* (MO); Trapiche, Perlas I, *Allen 2611*, (MO); *Johansen 112* (US), *Erlanson 432* (US); Panama Viejo, *Christopherson 173* (US); Nuevo San Francisco, *Standley 30777* (US); Bella Vista, *Maxon & Valentine 6956* (US); Panama, *Hayes 672* (BM). PROVINCE UNKNOWN: s. loc., *Seemann s.n.* (BM, K).

32. HURA

Hura L., Sp. Pl. 1008, 1753; Gen. Pl. ed 5, 439, 1754.

Trees, trunk with hard conical spines; monoecious. *Leaves* alternate, simple, long-petiolate, with 2 round glands at junction with blade; stipules caducous. *Inflorescences* unisexual. *Staminate flowers* in terminal long-pedunculate fleshy conical spikes, each flower sheathed by a membranous bract which ruptures at anthesis, sessile; calyx cupulate, denticulate; disc absent; stamens numerous, the filaments connate, the anthers in 2-several verticels, longitudinally dehiscent; pollen grains oblate, ternate, 3-colporate. *Pistillate flowers* solitary in uppermost leaf axils or rarely at base of male spike, long-pedicillate; calyx broad-cupulate, 5-toothed to subentire; disc absent; ovary of 5-20 carpels, each with a single ovule, the styles connate into a long column, dilated into radiating lobes at the apex. *Fruit* an explosively dehiscing woody capsule; seeds laterally compressed, ecaruncu-late.

Two neotropical species, widely planted as living fence posts. Only one has been collected in Panama.

1. **Hura crepitans** L., Sp. Pl. 1008, 1753.—Fig. 24.

Trees to 25 m, but often kept much lower when used as living fence posts. *Leaves* on petioles to 20 cm long; blade ovate to orbicular, 12-25 cm long and 7-15 cm wide, prominently penninerved, sparsely long-pubescent on the lower surface, the base cordate, the margin crenate with teeth often glandular tipped, the apex acuminate to subcuspidate. *Staminate flowers* 60-80 on conical fleshy axis 2-4.5 cm long, peduncle to 10 cm long; calyx to 1 mm long; staminal column to 2 mm long with 2-3 verticels of anthers, the third rarely complete. *Pistillate flowers* with pedicels to 5 cm long; calyx 3-5 mm long, truncate, or rarely shallowly 5-toothed; stylar column 2.5-5 cm long, the fleshy apical disc to 1 cm diam with radiating tips an additional 1 cm long. *Capsule* woody, oblate, to ca 8 cm diam, 3-5 cm long, dehiscing explosively into ca 15 crescentic cocci; seeds smooth, flattened, sub-orbicular, to 2 cm diam.

Costa Rica, the West Indies, Panama to tropical South America.

The other species, *H. polyandra* Baillon, is easily distinguished by the several verticels of anthers in its male flowers. There are no obvious vegetative differences but the range of this species seems to lie north of that of *H. crepitans* with overlap chiefly in Costa Rica.

BOCAS DEL TORO: Changuinola to 5 mi S at junction, Ríos Changuinola & Terebe, *Lewis et al. 832* (GH, MO, UC, US); vic of Chiriquí Lagoon, *von Wedel 1165* (MO), *1519* (MO), *2466* (MO), *2638* (MO), *2750* (MO), *Seibert 1561* (US). CANAL ZONE: Ancon,

Fig. 24. *Hura crepitans* L.: A, habit (×½); B, male flower (×10). A after *Allen 280* (MO); B after *Allen 4591* (MO).

Harvey 5247 (F); Balboa, *Standley 30855* (US); Barro Colorado I, *Aviles 5000* (F), *Wetmore & Abbe 224* (A, F), *225* (F, GH), *Shattuck 85* (A, F, MO), *370* (F), *Woodson & Schery 979*, (F, MO); Chagres, *Fendler 456* (MO); Darien Sta, *Standley 31627* (US); Gatun, *Ostenfeld 72* (C, US); Obispo, *Standley 31674* (US); Road C21, *Duke 5785* (MO); s. loc. *Hayes 792* (NY). CHIRIQUÍ: Progreso, *Cooper & Slater 273* (US). DARIEN: vic of Marraganti, *Williams 650* (NY, US); trail betw Pinogana & Yavisa, *Allen 280* (A, F, MO); Río Chico, vic of Yavisa, *Allen 4591* (MO). LOS SANTOS: Río Tonosi, vic of Tonosi, *Lewis et al. 1550* (MO), *1551* (GH, MO, US); Tonosi, *Tyson et al. 3105* (MO). PANAMA: Boyd Roosevelt Hwy, 1 mi N of Chagres River, *Blum & Tyson 1984* (MO); Corozal Rd, nr Panama, *Standley 26887* (US); beach from Panama Viejo to Bella Vista, *Allen 830* (MO).

33. EUPHORBIA

Euphorbia L., Sp. Pl. 450, 1753; Gen. Pl. ed 5, 208, 1754.

Herbs shrubs or trees, sometimes succulent, milky latex in all parts; monoecious or rarely dioecious. *Leaves* opposite, whorled or alternate, often serially on the same plant, simple; sometimes caducous particularly in succulent forms; usually petiolate except in succulents; stipules present or absent, sometimes glandular. *Inflorescence* a cyathium, the 5 cup-like lobes alternating at their tips with 4-5 glands, these with or without appendages. *Staminate flowers* in 4-5 cymes, the subtending bracteoles partly fused to the involucre or reduced or absent; naked; monandrous; pollen grains subglobose, reticulate to tectate, 3-colporate, sometimes operculate. *Pistillate flowers* terminal, solitary; perianth of 3-6 united sepals or absent; ovary 3-celled each with a single ovule, the styles 3, free or joined basally, usually partly bifid. *Fruit* capsular (rarely drupaceous); seed ± ovoid, angled or terete, the surface smooth or variously sculptured, with or without caruncle.

A genus of about 1200 species as used here. The diversity of plant form and detail of the reproductive structures have led a number of workers to suggest that the strong unifying feature of the cyathial inflorescence would better be considered a tribal than a generic character; a number of more "natural" genera would then be formed as segregates of the Linnaean *Euphorbia*. The most recent discussion of this, a fine account by Webster with a full bibliography (Jour. Arnold Arb. **48:** 303-430, 1967), takes the reasonable position that until such segregates can be defined in an unequivocal way they should not be separated as genera even though these would represent evolutionary units. Webster allows that a diagnosis can be made of *Chamaesyce* and accepts it "diffidently" as a genus, but treats all other segregates which have been proposed as part of *Euphorbia* L. Much the same disposition is made here. I have less hesitation in accepting *Chamaesyce* as a distinct genus, and have also accepted *Poinsettia* at that rank even though in Central America as a whole the boundary between this taxon and *Euphorbia* subg. *Agaloma* (Raf.) House is not always distinct. In Panama these two genera are easily distinguishable in the field, and I feel that it is more informative to treat them in this way than to maintain them in *Euphorbia* L.

a. Leaves all whorled; trees or large shrubs; stems articulate .....1. *E. cotinifolia*
aa. Leaves alternate, opposite or both, sometimes also with a whorl at one node; herbs, often vining; stems not obviously articulate.
  b. Capsule glabrous.

c. Seed terete, surface smooth; cyathia ca 2 mm diam, the glands 4, dark, the appendages equaling glands, ciliate-pubescent above .....2. *E. dwyeri*
cc. Seed strongly angled, surface deeply punctate with pits in regular longitudinal rows; cyathia ca 1 mm diam, the glands 4 or 2, green, the appendages obsolete (panamanian specimens) to prominent and white several times size of gland, glabrous .....3. *E. graminea*
bb. Capsule pubescent, especially when young.
d. Leaves ovate to subcordate, rarely larger than 1 × 1 cm; glands usually 4, appendages deeply 3-4 parted; capsule ca 1.5 mm diam; seed ca 1 mm long, surface deeply pitted .....4. *E. ocymoidea*
dd. Leaves ovate-lanceolate 3.5-6 × 1-2 cm; glands 2, appendages entire or obsolete; capsule ca 3 mm diam; seed ca 2.5 mm long, surface papillate .....5. *E. oerstediana*

1. **Euphorbia cotinifolia** L., Sp. Pl. 453, 1753.

Tree, head strongly branched, to 10 m, branches terete, articulate, glabrous. *Leaves* ternate (rarely alternate at some nodes); stipules obsolete; petiole 2-6 cm long, slender; blade ovate, 4-6 × 3-5 cm, green, glabrous or with scattered short hairs, the base rounded, sometimes obscurely peltate, the margin entire, the apex truncate to emarginate. *Cyathia* in terminal cymes, often forming showy panicles with up to 30 on each of 6-12 laterals at the tip of a branch, campanulate, ca 3 mm diam, the lobes broad, fimbriate and often white at their apices; glands 5(4), brown, the appendages larger than glands, white. *Fruit* not seen from Panamanian material; a Mexican collection (*Pringle 6069* MO) has capsules broadly ovoid, to 6 mm diam, sparsely pubescent; seed ovoid, ca 2.5 mm long, somewhat angled, the surface deeply pitted with pits ± in rows and occasionally also warted, ecarunculate.

Mexico through Central America to northern South America. Occasionally planted as living fence posts and probably introduced to the West Indies for this reason.

CHIRIQUÍ: nr Francés Arriba school, ca 14 mi N of David, *Lewis et al. 661* (DUKE, F, GH, K, MO, NY, UC, US); vic of San Felix, *Pittier 5449* (F, US).

A very striking small tree similar to this taxon but with bright red leaves is often seen in Central America as a hedge plant. An example from Panama is *Duke 8454* (MO) from a cemetery in Mulatuppu, Comarca de San Blas. Its taxonomic position is not clear but it is probably the entity which Klotzsch & Garcke described as *Alectoroctonum caracasanum* (Abh. Akad. Berlin, Phys.-Math. **1860:** 40, 1860). In making the transfer to *Euphorbia* Boissier (in DC., Prodr. **15**(2): 60, 1862) describes it as having cymes of 3-7 cyathia. This and the color and possibly thinner texture of the leaves may be enough to warrant its separation at specific rank, but further collections from all parts of the range are needed to be sure whether this is the case or if it would better be treated as a subspecific segregate of *E. cotinifolia*.

2. **Euphorbia dwyeri** Burch, Ann. Missouri Bot. Gard. **54:** 182, *fig. 1*, 1967.

Herb, stems terete, glabrous, not articulate, sparingly branched, sprawling, to 1.5 m long. *Leaves* alternate through most of plant, opposite above a 3-leaved whorl; stipules obsolete; petiole 2.5-6 cm long, slender; blade ovate-lanceolate, 3.5-6 × 2-3.5 cm, thin, green (drying darker above than below), glabrous except for scattered short hairs on the under surface, the base cuneate to rounded, sometimes obscurely peltate, the margin entire, the apex obtuse to rounded or emarginate and mucronulate. *Cyathia* in groups of 2-5 on short dichotomizing laterals, funnelform-campanulate, 2 mm long, 2 mm in diam; peduncle to 4 mm long; glands 4, dark, the appendages equaling glands and with short spreading hairs on upper surface simulating a ciliate edge to the gland, occasionally glabrous. *Capsule* broadly ovoid, 4 × 4 mm, glabrous; seed ovoid, 3 mm long, smooth, terete, ecarunculate.

Known only from the type collection from a trail to the lower edge of a cloud forest at an altitude of 5000-5800 ft.

CHIRIQUÍ: Cerro Horqueta, NW of Boquete, *Dwyer et al. 434* (holotype MO; isotypes GH, K, US).

3. **Euphorbia graminea** Jacquin, Sel. Stirp. Amer. 151, 1763.

E. picta Jacquin, Coll. **3:** 178, 1790.

Herb, stems terete, not articulate, branching from base, sprawling to 1.5 m long. *Leaves* alternate, becoming opposite above; stipules obsolete; petiole to 2 cm long; blade oblong-elliptic to sublinear or rarely ovate, 2.5-4(-8) × 0.5-1.5(-5) cm, green, short pubescent or glabrous, the base acute to obtuse, the margin entire, the apex acute. *Cyathia* terminal on dichotomizing upper branches, funnelform, ca 1 mm diam; glands 2-4, minute, exappendiculate (extra-Panamanian specimens often with large white appendages). *Capsule* broadly ovoid, ca 3.5 mm diam, glabrous; seed ovoid, 1.5 mm long, angular, deeply punctate with pits in regular longitudinal rows, ecarunculate.

Southern Mexico to northern South America. A very variable species in all parts of its range. It may, in fact, be a complex of separable taxa but many of the segregates made to date are unconvincing.

CANAL ZONE: Farfan beach area, *Tyson et al. 3171* (MO). DARIEN: trail from Río Pucro to Quebrada Maskia, *Duke 13054* (MO); vic of Yape, *Allen 860* (F, MO). PROVINCE UNKNOWN: s. loc., *Seemann 1241* (BM), *1649* (BM).

4. **Euphorbia ocymoidea** L., Sp. Pl. 453, 1753.

Herb, stem not articulate, much branched, scandent to 1 m. *Leaves* alternate at base, opposite above; stipules obsolete; petiole to 1.5 cm long, slender; blade broadly truncate-ovate to subcordate, ca 1 × 1 cm on main stems, much smaller on laterals, thin, sparsely long pubescent on each surface, the base truncate or short-acuminate, the margin entire, the apex obtuse. *Cyathia* terminal on branched laterals, campanulate, ca .75 mm diam; glands usually 4, the appendages

larger than gland, deeply 3-4-parted. *Capsule* ovoid, to 1.5 mm diam, long pubescent; seed ovoid, 1 mm long, angular, surface deeply pitted, ecarunculate.

Central America and probably northern South America.

CANAL ZONE: Farfan Beach area, *Tyson et al. 3170* (MO). HERRERA: rd from La Avena to Pesé, *Burch et al. 1289* (GH, MO, UC, US).

5. **Euphorbia oerstediana** (Kl. & Gke.) Boiss. in DC., Prodr. **15**(2): 59, 1862.

Poinsettia oerstediana Kl. & Gke., Monatsb. Akad. Berlin **1859:** 253, 1859.

Herb, stems terete, glabrous except at tips, not fully articulate, sparingly branched, erect to 9 inches. *Leaves* alternate, sometimes opposite near apex of stems; stipules obsolete; petiole ca 1 cm long; blade thin, ovate-lanceolate, 3.5-6 × 1-2 cm, scattered short hairs on each surface, the base obtuse to rounded, the margin entire, the apex obtuse to mucronate. *Cyathia* in small terminal groups, campanulate, ca 1 mm diam; glands 2, the appendages green, the margins entire, upright or obsolete. *Capsule* broadly ovoid, ca 3 mm diam, densely pubescent particularly when young; seed ovoid, 2.5 mm long, surface papillate, minutely carunculate.

Central America, West Indies and northern South America. Known from only one collection in Panama, but probably more common than this would indicate and simply overlooked since it is a very inconspicuous member of the flora of wooded areas.

HERRARA: rd from La Avena to Pesé, *Burch et al. 1316* (MO).

Another species, *E. apocynoides,* was described by Klotzsch on the basis of material collected by Seemann (in Seemann, Bot. Voy. Herald 99, 1853). The only material seen, a probable type sheet from BM, is not full enough to allow a decision on its identity. The leaves suggest the Mexican *E. fulgens* Karwinsky, but the single cyathium present is closer to that of the group containing *E. oerstediana* and *E. lancifolia* Schlecht. (Boissier's sect. *Dichilium*); Klotzsch's description, on the other hand, stresses the articulation of the stems which suggests sect. *Alectoroctonum.* No sensible disposition can be made of this taxon until more material is available and it is to be hoped that the increased collecting activity in the Republic will continue to add to our knowledge of this genus.

34. POINSETTIA

Poinsettia Graham, Edinb. New Philos. Jour. **20:** 412, 1836.

Euphorbia sect. *Poinsettia* (Graham) Baillon, Étude générale du groupe des Euphorbiacées 284, 1858.

Herbs, annual or perennating, or shrubs, milky latex in all parts; monoecious. *Leaves* opposite or alternate; petiolate; stipules absent or minute; blades expanded, green, those subtending the inflorescences ("floral bracts") red, purple, or white in some species. *Inflorescence* a cyathium, these in terminal condensed dichasia or pleiochasia; lobes 5, the involucral glands cup-like, exappendiculate, usually

one but rarely up to 5 in central cyathia. *Staminate flowers* few to many; naked; monandrous; pollen grains subglobose, usually tectate, 3-colporate. *Pistillate flower* terminal, solitary; naked; ovary 3-celled, each with a single ovule, the styles 3, joined at base, bifid for most of length. *Fruit* a capsule dehiscent at sutures; seed ovoid, somewhat angled, surface variously sculptured, the caruncle small or absent.

A New World genus of about 12 species, probably centered in Mexico. Two of the weedy species are found wild in Panama and a third, *P. pulcherrima* (Graham) Willd., is widely cultivated for its showy bracts. This species, "Poinsettia" of the florist trade and "flor de Pascua" in most of Latin America, is a large shrub with brilliant red, pink or white leaves subtending the inflorescence, and with cyathia 5 mm or more in diameter. It may well be naturalized in the Republic.

Useful reference:

Dressler, R. L., A synopsis of *Poinsettia* (*Euphorbiaceae*). Ann. Missouri Bot. Gard. **48:** 329-341, 1962.

a. Cyathial gland with a circular opening; floral bracts green or purple spotted but never red at the base; seed angular ..... 1. *P. heterophylla*
aa. Cyathial gland bilabiate; floral bracts green or red at base; seed not strongly angled ..... 2. *P. cyathophora*

1. **Poinsettia heterophylla** (L.) Kl. & Gke., Monatsb. Akad. Berlin **1859:** 253, 1859.—Fig. 25 (A, B).

Euphorbia heterophylla L., Sp. Pl. 453, 1753.
E. geniculata Ortega, Hort. Mat. Dec. 18, 1797.
E. morisoniana Kl. in Seemann, Bot. Voy. Herald 100, 1853.

Herb, annual or perennating. *Stem* ascending, to 7 dm long, dark green. *Leaves* alternate at base, opposite above; blades membranous, 5-11 × 2-5 cm, pandurate, obovate or elliptic, rarely lanceolate, entire or dentate, glabrous or hairy, green sometimes purple-splashed or pale at the base but never red. *Cyathia* glabrous without, the gland stipitate, terete with a slightly flared round opening. *Capsule* glabrous, broadly truncate-ovoid, to 4 mm long, 5 mm wide; seed truncate-ellipsoid, to 2.5 mm long, somewhat angular, the surface coarsely tuberculate.

Widely distributed as a weed in tropical America, and extending into Florida, Louisiana and Texas.

BOCAS DEL TORO: Almirante, *Cooper 122* (F), *Seibert 1536* (MO); Bocas del Toro, *Carleton 94* (F, US); Changuinola, *Dunlap 384* (F, US), *Lewis et al. 815* (GH, MO, UC, US); Chiriquicito to 5 mi S along Río Guaramo, *Lewis et al. 1990* (GH, MO). CANAL ZONE: outskirts of Ancon, *Greenman & Greenman* 5072 (MO); Barro Colorado I, *Ebinger 146* (MO, US), *Shattuck 70* (F), *Starry 192* (F), *Woodworth & Vestal 410* (F); nr beach at Fort Kobbe, *Duke 4711* (MO); Gatun Station, *Tyson 2274* (MO); Miraflores, *White 144* (F, MO). CHIRIQUÍ: vic of Boquete, *Davidson 729* (F), *Lewis et al. 599* (GH, K, MO, UC, US); vic of Puerto Armuelles, *Woodson & Schery 842* (F, MO). COCLÉ: betw Aguadulce & Antón, *Woodson et al. 1216* (F, MO); banks of Río Grande, *Burch et al. 1181* (MO). HERRERA: rd from Chitré to Divisa, *Burch et al. 1362* (GH, MO). PANAMA: nr Arraijan, *Woodson et al. 1368* (F, MO); betw Panama & Chepo, *Dodge et al. 16661* (MO); InterAmer Hwy E of Bejuco, *Duke 4557* (MO); Río Charco-Espiritu on Tocumen Hwy, *Duke 5700* (MO); Taboga I, *McBride 2836* (F).

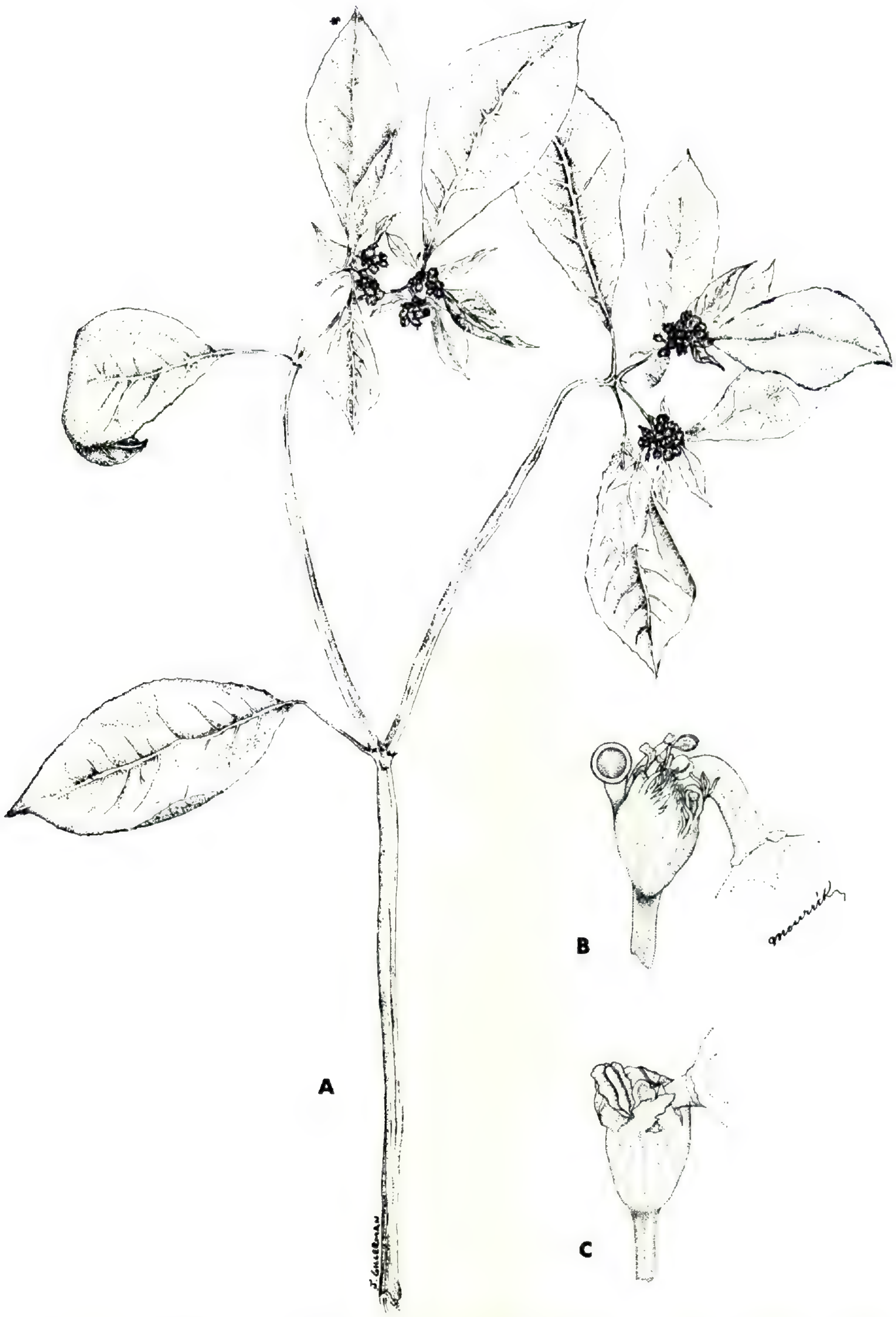

Fig. 25. *Poinsettia heterophylla* (L.) Kl. & Gke.: A, habit (×½); B, cyathium (×6). A-B after *Siebert 1536* (MO). *P. cyathophora* (Murray) Kl. & Gke.: C, cyathium (×6). C after *Lewis et al.* 682 (MO).

2. **Poinsettia cyathophora** (Murray) Kl. & Gke., Monatsb. Akad. Berlin **1859:** 253, 1859.—Fig. 25(C).

Euphorbia cyathophora Murray, Comm. Götting. **7:** 81, 1786.
E. heterophylla β *cyathophora* (Murray) Boiss. in DC., Prodr. **15**(2): 72, 1862.

Herb, annual or perennating. *Stems* ascending, to 5 dm long (one collection to 16 dm), green, somewhat glaucous. *Leaves* alternate at base of plant, opposite above; blades membranous, 5-10 × 1-3 cm, pandurate, ovate, lanceolate or sublinear, entire or dentate, glabrous or sparsely long-hairy, green, those subtending the inflorescence often bright red at the base or throughout. *Cyathia* glabrous or sparingly short-pubescent, the gland flattened, strongly bilabiate. *Capsule* glabrous, broadly ovoid, to 4 mm long, 5 mm wide; seed truncate-ellipsoid, to 3 mm long, scarcely angled, the surface tuberculate.

Common in waste places in the eastern United States and the West Indies, present as a weed of disturbed areas in much of the remainder of the United States, Central America and northern South America, as well as parts of the Old World.

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 1313* (MO), *2607* (MO), *2926* (MO); Isla Colón, *von Wedel 139* (MO); Careening Cay, *von Wedel 575* (MO). CHIRIQUÍ: ca 14 mi N of David, *Lewis et al. 682* (MO).

This species is much less common than *P. heterophylla* in Panama, which upholds Dressler's observation (loc. cit.) of the relative frequency of the two in the tropics.

Each of the two species shows great variation in vegetative characters, particularly leaf shape, but observations in the field do not support the authors who have separated and named taxa on this basis.

35. CHAMAESYCE

Chamaesyce S. F. Gray, Nat. Arr. Brit. Pl. **2:** 260, 1821.

Anisophyllum Haworth, Syn. Pl. Succ. 1959, 1812, non Jacquin (Sel. Stirp. Amer. Hist. 283, *t. 180, fig. 45,* 1763).
Euphorbia sect. *Anisophyllum* Roeper in Duby, A.P. D.C., Bot. Gall. ed 2, **1:** 412, 1828.

Herbs or subshrubs, annual or short perennating, prostrate to ascending or erect, milky latex in all parts; monoecious; the main axis aborting, the secondary axes few to many, rarely rooting at nodes. *Leaves* opposite, simple; petiolate with stipules interpetiolar, distinct or joined; blades expanded, with chlorophyll-bearing cells mainly in a sheath around veins and colorless areas in between, the base inequilateral, the margin entire or serrate. *Cyathia* terminal but appearing axillary, solitary at nodes or clustered in cymules; lobes 5 approximating glands; glands 4 or with fifth vestigial, alternating with lobes, with petaloid appendages (these rarely obsolete). *Staminate flowers* few to many; naked; monandrous; pollen grains subglobose, tectate, 3-colporate. *Pistillate flowers* terminal, solitary; naked; ovary 3-celled each with a single ovule, the styles 3, free or joined basally, partly bifid. *Fruit* capsular, almost always fully exerted and not splitting cyathium

at maturity; seed ovoid, angled or terete, the coat smooth or variously sculptured, ecarunculate.

Plants of disturbed habitats, most abundant in rather dry situations and succumbing quickly to competition in more favorable sites.

A genus of about 250 species, of world-wide distribution but with by far the largest number of species in the New World. The genus is poorly represented in Panama by comparison with neighbouring countries, and of the 10 species found six are known from five or fewer collections of each.

Recent works include:

Wheeler, L. C., *Euphorbia* subgenus *Chamaesyce* in Canada and the United States exclusive of Canada. Rhodora **43:** 97-154, 168-205, 223-286, 1941 (Reprinted as Contr. Gray Herb., Harvard Univ. **136**).

Burch, D. G., Two new species of *Chamaesyce* (*Euphorbiaceae*), new combinations, and a key to the Caribbean members of the genus. Ann. Missouri Bot. Gard. **53:** 90-99, 1966.

a. Capsule pubescent, at least when young.
  b. Plant erect or ascending; cyathia in short-stalked leafy dichasia .....1. *C. lasiocarpa*
  bb. Plant prostrate or decumbent; cyathia in glomerules or on condensed leafy laterals.
    c. Cyathia borne in dense lateral and terminal leafless glomerules .....2. *C. hirta*
    cc. Cyathia borne on condensed leafy laterals.
      d. Capsule not fully exserted, splitting cyathium at maturity; glands subcircular, appendages usually all equal in size .....3. *C. thymifolia*
      dd. Capsule fully exserted and not splitting cyathium at maturity; glands rimming cyathium, appendages unequal in size with one pair very long and often concealing capsule.
        e. Glandular appendages pubescent on underside .....4. *C. densiflora*
        ee. Glandular appendages glabrous on underside .....5. *C. dioica*

aa. Capsule glabrous.
  f. Leaf margins entire.
    g. Plants prostrate to decumbent; stipules distinct, deeply lanciniate .....6. *C. ammannioides*
    gg. Plants erect to sprawling; stipules united, short-cleft or fringed .....7. *C. buxifolia*
  ff. Leaf margins serrate, at least in upper $\frac{1}{3}$.
    h. Capsule more than 2 mm long; seed to 1.8 mm long .....8. *C. bahiensis*
    hh. Capsule less than 2 mm long; seed rarely longer than 1 mm.
      i. Cyathia in almost leafless lateral and terminal glomerules; capsule subspherical, less than 1.4 mm long .....9. *C. hypericifolia*
      ii. Cyathia in leafy lateral and terminal dichasia; capsule oblong-ovoid, more than 1.6 mm long .....10. *C. hyssopifolia*

Three other common weeds of the American tropics are to be expected in Panama: *C. ophthalmica* (Pers.) Burch is like a delicate plant of *C. hirta*, but may be distinguished by the position of its glomerules of cyathia which are always terminal; *C. prostrata* (Ait.) Small and C. serpens (H.B.K.) Small are each small prostrate plants. The first is easily distinguished by its capsule, stiff-hairy only on the angles, and the second by its joined, scale-like white stipules and the fact that it frequently roots at the nodes.

1. **Chamaesyce lasiocarpa** (Kl.) Arthur, Torreya **11:** 260, 1911.

Euphorbia lasiocarpa Kl., Nov. Act. Leop. **19,** suppl. 1:414, 1843.

Herb, annual, ascending to 5 dm. *Stems* to 4 mm diam at woody base, densely tomentose. *Leaves* membranous; stipules joined, deltoid, tufted or deeply bifid; blades ovate-lanceolate somewhat falcate, 8-20 × 3-4 mm, densely gray-pubescent, the base rounded, the margin sharp-serrate, the apex acute to obtuse. *Cyathia* solitary in lateral and terminal short-stalked, leafy dichasia, densely pubescent; glands small, the appendages to three times as long and broad as gland, white, or obsolete. *Capsule* tomentose, sometimes glabrate, broadly ovoid, 1.5-2 × 2 mm; seeds oblong-ovoid, to 1 mm long, strongly 4-angled, the faces flat with 2-4 deep transverse ridges.

Greater Antilles, Central America and northern South America. Only three Panama collections can be placed with assurance under this name. Even these are rather closer in appearance to *C. hyssopifolia* (from which it differs chiefly in pubescence) than is usual over most of the range of the two species.

CANAL ZONE: Corozal to Pedro Miguel, *Cowell 407* (F, NY). LOS SANTOS: 3 mi S of Carreta, *Burch et al. 1234* (F, GH, K, MO, UC, US). PANAMA: Panama Viejo, *Duke 5732a* (MO).

2. **Chamaesyce hirta** (L.) Millsp., Publ. Field Mus. Nat Hist., Bot. Ser. **2:** 303, 1909.

Euphorbia hirta L., Sp. Pl. 454, 1753.
E. globulifera H.B.K., Nov. Gen. Sp. Pl., **2:** 56, 1817.

Herb, annual; decumbent to 3 dm. *Stems* few, to 2 mm diam, tomentose and with abundant multicellular hairs which are often brown or purple, rarely merely tomentose. *Leaves* membranous; stipules distinct or joined at base, somewhat lacerate, to 1 mm long; blades ovate to lanceolate, often rhombiform, 10-35(-55) × 5-15(-25) mm, glabrate on upper surface, green or red often with purple spot, the base rounded to cuneate, the margin serrate, the apex obtuse to acute. *Cyathia* in dense terminal and axillary glomerules formed of condensed leafless dichasia, strigose; glands minute, purple, the appendages obsolete to three times as wide as gland. *Capsule* strigose, ovid, to 1 mm long, 1 mm wide; seed cuneiform, 0-8 mm long, 0.4 mm wide above base, the angles subequal, the faces concave, obscurely transversely ridged or wrinkled, tan, red-brown or gray.

A pantropical weed. Widespread and extremely common in all disturbed areas in Panama.

BOCAS DEL TORO: Bocas del Toro I Airport, *Lewis et al. 787* (MO, UC, US); vic of Chiriquí Lagoon, *von Wedel 539* (MO); Old Bank I *von Wedel 1868* (MO); Water Valley, *von Wedel 1748* (MO). CANAL ZONE: Ancon, *Greenman & Greenman 5009* (MO); western slope of Ancon Hill, *Seibert 111* (MO); Barro Colorado I, *Hayden 1* (MO), *McDaniel 5027* (FSU, MO), *Woodworth & Vestal 408* (F); id, Miller Trail, *Shattuck 41* (F); vic of Corrosion Lab, *Duke 4441* (DAV, MO), *Stern et al. 63* (MO); Chagres, Isthmus of Panama, *Fendler 274* (BM, K, MO, W); Culebra I, *Duke 4632* (DAV, MO); Fort Clayton, Cardenas Creek area, *Tyson 1290* (FSU), *Dwyer 2787* (MO); Fort Kobbe, *Duke 3907* (MO), *3932* (MO), *Woodson et al. 1429* (F); Fort San Lorenzo, *Burch et al.*

1029 (GH, K, MO, UC, US); E of Gatun locks, *Duke 4298* (DAV); Gamboa, *Petersen s.n.* (F); vic of Salamanca Hydrographic Sta, Río Pequeni, *Woodson et al. 1616* (F, MO); Sosa Hill, *Duke 4659* (DAV, MO). CHIRIQUÍ: David airport, *Lewis et al. 744* (GH, K, MO, UC, US). COCLÉ: Río Hato airstrip, *Burch et al. 1140* (F, GH, K, MO, NY). COLÓN: Colón, vacant lot, *MacBride & Featherstone 5* (F), *Rodway s.n.* (K); 2.4 mi S of Piña, *Lewis et al. 1850* (GH, MO, US). DARIEN: vic of Boca de Cupe, *Allen 893* (F, MO); El Real, *Burch et al. 1053* (GH, MO, US); Río Sabana, *Léopold III 106* (MO); 2 mi E Santa Fe, *Tyson et al. 4826* (MO); vic of Santa Fe, *Duke 9486* (MO). HERRERA: Rd from La Avena to Pesé, *Burch et al. 1286* (MO, UC); banks of Río Santa Maria, *Burch et al. 1200* (GH, MO); rd betw Las Minas & Pesé, *Burch et al. 1346* (K, MO), *1348* (GH, MO, UC, US); 12.5 mi S of Ocú, *Lewis et al. 1660* (GH, MO, US). LOS SANTOS: Playa de la Concepción, *Burch et al. 1263* (F, GH, MO, NY). PANAMA: Isla Taboga, *Woodson et al. 1502* (F, MO); Panama City, *Petersen s.n.* (F); rd to Ojus de Agua, ca 5 mi N of Panama City, *Stimson 5052* (DUKE, MO).

3. **Chamaesyce thymifolia** (L.) Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. **2:** 412, 1916.

Euphorbia thymifolia L., Sp. Pl. 454, 1753.

Herb, annual, perennating by thick rootstock, prostrate, forming mats to 4 dm diam. *Stems* 1-2 mm thick, villous-pubescent or tomentose on upper surface, often glabrate, naked on under surface, green or light brown. *Leaves* membranous; stipules distinct, linear, toothed; blades oblong-elliptic, 4-10 × 2-5 mm, the upper surface usually glabrous, the lower sparsely tomentose, glabrate, green or yellowish, the base oblique or subequilateral on side shoots, the margin coarsely serrate, the apex rounded to acute. *Cyathia* solitary or in pairs or even few-flowered glomerules at nodes of condensed leafy laterals; glands broadly elliptic or subcircular, pink or red, the appendages small. *Capsule* strigose, long-ovoid, 0.8-1 mm long, 1 mm wide below equator, not fully exserted but splitting cyathium at maturity; seed conical-ovoid, to 0.9 mm long, 0.5 mm wide below equator, strongly 4-angled, the faces concave, obscurely transversely ridged, tan-colored.

New World tropics and subtropics. Widespread and common in the Republic. Its small size allows it to survive in places in which the larger weedy species would be damaged.

BOCAS DEL TORO: Bocas del Toro I airport, *Lewis et al. 783* (GH, K, MO, UC, US), *784* (DUKE, F, GH, MO), Little Bocas, vic of Chiriquí Lagoon, *von Wedel 2487A* (MO); Changuinola, Lewis *et al. 939* (GH, MO), *Dunlap 85* (F, US); 10-15 mi S of mouth of Changuinola River, *Lewis et al. 820* (F, K, MO, NY, UC, US). CANAL ZONE: Chagres, Isthmus of Panama, *Fendler 278* (BM, F, K, MO, W); Coco Solo, *Elias & Kirkbride 1625* (MO); Farfan Beach, *Burch et al. 1406* (MO); Fort Clayton, *Stimson 5041* (DUKE, MO); Fort Sherman, *Duke 4369* (DAV, MO); Frijoles Station, *Stimson 5273* (DUKE, MO); Gatun, *Hayes 674* (F, NY); nr Miraflores lock, *Stimson 5215* (DUKE, MO). CHIRIQUÍ: David airport, *Lewis et al. 734* (F, GH, K, MO, NY, UC, US). COCLÉ: Nata, *Allen 828* (F, MO); Río Hato airstrip, *Burch et al. 1156* (MO). COLÓN: 2.4 mi SW of Piña, *Lewis et al. 1848* (MO), *1849* (GH, MO, US). DARIEN: vic of Boca de Cupe, *Allen 896* (MO); El Real, *Burch et al. 1054* (MO); Río Tuqueza, vic of Boca Quebrada Venado, *Bristan 1099* (MO). HERRERA: Rd betw Las Minas & Pesé, *Burch et al. 1343* (GH, MO, US). LOS SANTOS: 17.8 mi S of Macaracas, *Lewis et al. 1599* (GH, MO, US). PROVINCE UNKNOWN: s. loc., *Seemann 194* (BM).

4. **Chamaesyce densiflora** (Kl. & Gke.) Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. **2:** 391, 1914.—Fig. 26.

Anisophyllum densiflorum Kl. & Gke., Monatsb. Akad. Berlin **1859:** 28, 1859.
Euphorbia densiflora (Kl. & Gke.) Kl. in Peters, Reise Mossamb. 94, 1862.

Herb, annual or perennating, prostrate or decumbent. *Stems* 1-2 mm thick, densely long-pubescent particularly at sides, hairs multicellular, often purple. *Leaves* membranous; stipules distinct, sublinear; blades obliquely oblong, 10-20 × 5-9 mm, sparsely pubescent, the base strongly oblique, the margin serrate, the apex obtuse. *Cyathia* densely clustered on short leafy laterals, white-pubescent; glands rimming cyathium, one pair often obsolete, deep red, the appendages in two unequal pairs, one a mere rim to their glands (or absent when glands are obsolete), the other auriculate and extended laterally, deep red, pubescent on lower surface, often concealing capsule. *Capsule* densely pubescent, broadly ovoid to 1.8 mm long; seeds angular-ovoid, ca 1 mm long, the faces deeply transversely ridged.

Central America and northern South America. Not uncommon in the Republic but probably confined to the medium altitude regions in which it has already been collected.

CHIRIQUÍ: vic of Boquete, *Lewis et al. 328* (GH, K, MO, UC, US), *Pittier 2848* (F). HERRERA: roadside betw Las Minas & Pesé, *Burch et al. 1347* (GH, MO, UC, US).

5. **Chamaesyce dioica** (H.B.K.) Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. **2:** 384, 1914.

Euphorbia dioeca H.B.K., Nov. Gen. Sp. Pl. **2:** 53, 1817.

Herb, perennial or at least perennating, prostrate in dense mats. *Stems* to 1 mm thick, wooly-pubescent. *Leaves* membranous; stipules distinct, linear; blades elliptic, ca 4 mm long, 1-1.3 mm wide, sparsely pubescent on each side, the base acute, the margin serrate, the apex acute. *Cyathia* solitary at nodes of short condensed laterals, densely pubescent; glands elliptical, rimming cyathium, the two pairs sometimes unequal, dark red, the appendages in two unequal pairs, the larger pair auriculate, glabrous, often concealing capsule. *Capsule* and seed not seen from Panama—capsule pubescent, ovoid, ca 1.4 mm long; seed angular-ovoid with lateral ridges in South American specimens.

Probably restricted to South and Central America but part of a closely related group that extends into the West Indies and southern United States. This species is included reluctantly on the basis of a single collection which is too sparse to be absolutely certain that it is not an extreme form of *C. thymifolia.*

COCLÉ: Río Hato reservation, InterAmer Hwy, *Tyson & Blum 2555* (MO).

6. **Chamaesyce ammannioides** (H.B.K.) Small, Fl. SE. U.S. 709, 1903.

Euphorbia ammannioides H.B.K., Nov. Gen. Sp. Pl. **2:** 55, 1817.

Herb, annual or perennating, prostrate or decumbent forming loose mats to 6 dm diam. *Stems* 1-2 mm thick, not rooting at nodes, glaucous, often suffused

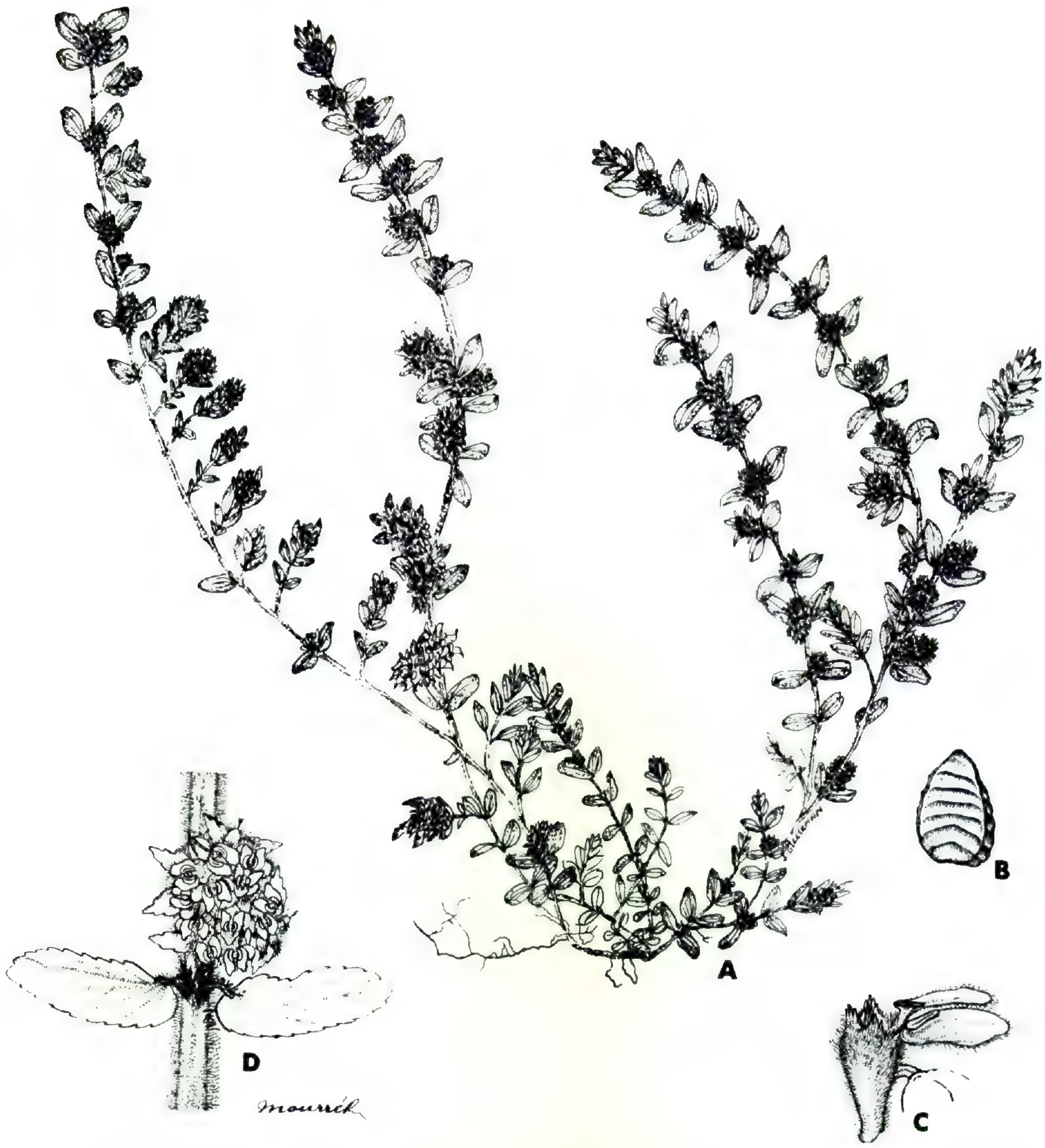

Fig. 26. *Chamaesyce densiflora* (Kl. & Gke.) Millsp.: A, habit (×½); B, seed (×12); C, cyathium (×8); D, cyathia on condensed lateral (×1½). After *Lewis et al.* 328 (MO).

red. *Leaves* often slightly fleshy; stipules distinct, deeply laciniate into 3-6 linear segments; blades oblong-elliptic, 6-12 × 2.5-6 mm, glaucous often suffused red, the base obtuse, the margin entire, the apex obtuse to mucronate. *Cyathia* solitary, terminal on branches of lateral shoots near tips of main stems, glabrous; glands subcircular, somewhat stipitate, the appendages usually obsolete. *Capsule* glabrous, broadly ovoid, 1.8-2.1 × 2-2.4 mm; seed ovoid, to 1.8 mm long, 1.3 mm diam at equator, obscurely 3-angled from apex for ca ½ length, terete at base, smooth, white.

Coastal sands of Florida, Mexico, Cuba, Guatemala and northern South America. Represented from Panama by only two collections.

CANAL ZONE: Chagres, *Fendler* 276 (F, K, MO), 277 pro parte (W—probably numbered in error). VERAGUAS: mouth of Río Concepción, *Lewis et al.* 2786 (MO).

7. **Chamaesyce buxifolia** (Lam.) Small, Fl. SE. U.S. 712, 1903.

Euphorbia buxifolia Lam., Encyc. Méth. Bot. **2:** 421, 1788.
E. litoralis H.B.K., Nov. Gen. Sp. Pl. **2:** 54, 1817.
E. flexuosa H.B.K., loc. cit. 55.

Subshrub, perennial, erect to ascending, nearly decumbent in shifting sand. *Stems* to 6 dm long, to 8 mm diam at naked woody base, glabrous, green becoming darker. *Leaves* somewhat fleshy; stipules united, to 1 mm long, ligulate or deltoid, short cleft or fringed, white; blades ovate to elliptic, 5-12 × 3-6 mm, glabrous, yellowish- to dark green and glaucous, the base truncate to cordate, obscuring stem, the margin entire, the apex obtuse. *Cyathia* solitary at upper nodes; glabrous without, densely ciliate in throat; glands transversely elliptic, brown, fleshy, the appendages as wide as gland, white, the margin entire or undulate. *Capsule* glabrous, subspherical 1.5-2 mm long, 2.2-5 mm wide; seed broadly ovoid, 1.3 mm long, 1.2 mm wide, the angles mere ridges except near apex, the faces plump, convex, the surface obscurely pitted, ashen.

Coastal sands of Florida, the Antilles, the Bahamas, Central America and northern South America.

Lamarck's name is retained for this species in spite of the case made for the adoption of *E. mesembrianthemifolia* Jacquin in recent floras of the West Indies and by Dugand when publishing the combination in *Chamaesyce* (Phytol. **13:** 385, 1966). While Jacquin's description (Enum. Pl. Carib. 22, 1760 and Sel. Stirp. Amer. 150, 1763) suggests that his epithet could be applied to this plant, no authentic material has been found, and I hesitate to upset a well-understood usage without some incontrovertible evidence.

BOCAS DEL TORO: Old Bank I, vic of Chiriquí Lagoon, *von Wedel 2130* (MO). SAN BLASS Sunset I, *Duke 8863* (MO); Irandi airport, *Duke 6509* (MO); Perme, *Cooper 226* (F). PROVINCE UNKNOWN: s. loc., *Pittier 4108* (F).

8. **Chamaesyce bahiensis** (Kl. & Gke.) Dugand & Burch, Caldasia, (in press).

Anisophyllum bahiense Kl. & Gke., Monatsb. Akad. Berlin **1859:** 33, 1859.
Euphorbia bahiensis (Kl. & Gke.) Boiss. in DC., Prodr. **15**(2): 24, 1862.

Herb, annual or perennating, trailing or erect to 5 dm. *Stems,* 2-4 mm diam, usually dark particularly at nodes. *Leaves* membranous; stipules joined, shortly-deltoid, fringed; blades oblong-elliptic to obovate 15-30 × 6-12 mm, those on laterals much smaller, glabrous, the base truncate or cordate, the margin serrate, sometimes obscurely so, the apex obtuse to rounded. *Cyathia* solitary in lateral dichasia, glabrous; glands elliptic, the appendages obsolete to prominent, white. *Capsule* glabrous, broadly ovoid, to 2.5 mm long, 3 mm diam; seed ovoid to 1.8 mm long, strongly 4-angled, the faces flat, wrinkled.

Coastal sands from Rio de Janeiro to Costa Rica with a single collection known from Jamaica. The Atlantic Coast of Panama has few of the sand beaches on the upper parts of which this plant grows but the recent intensive collecting produced two colonies and it would be surprising if more are not found as the remoter beaches are visited.

CANAL ZONE: 1 mi E of Piña, *Lewis et al. 1837* (MO). VERAGUAS: mouth of Río Concepción, *Lewis et al. 2773* (K, MO, NY, UC).

9. **Chamaesyce hypericifolia** (L.) Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. **2:** 302, 1909.

Euphorbia hypericifolia L., Sp. Pl. 454, 1753.
E. pilulifera L. sensu Wheeler, Contr. Gray Herb. **127:** 76, 1939. (but see disclaimer, loc. cit. 78).
C. glomerifera Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. **2:** 377, 1913.

Herb, annual or perennating, erect to ascending to 4 dm. *Stem* to 3 mm diam at somewhat woody base, tan to dark brown. *Leaves* membranous; stipules joined and sheathing with margin serrate, or, at upper nodes, separate, entire or deeply 2-4 cleft; blades ovate-elliptic to elliptic-obovate, somewhat falcate, 15-35 × 8-14 mm, glabrous, green, the base rounded or cuneate, the margin serrate, the apex acute. *Cyathia* in short-stalked, lateral and terminal congested dichasia forming glomerules with a few basal leaves, glabrous; glands subcircular, the appendages obsolete or prominent, entire, white or pink. *Capsule* glabrous, subspherical, to 1.2 mm diameter; seed ovoid, to 0.8 mm long, 0.5 mm wide, strongly 4-sided, the faces flat or convex, wrinkled, light brown.

New World tropics and subtropics. There are remarkably few collections from Panama of this plant which is extremely common in other parts of its range. The numbers of collections of this and the following species seem to be an accurate representation of their relative frequency and the plant is by no means common in the Republic.

BOCAS DEL TORO: Isla Colón, vic of Chiriquí Lagoon, *von Wedel 2829* (MO); Bocas del Toro I airport, *Lewis et al. 786* (GH, MO). CANAL ZONE: Ancon, *Greenman & Greenman 5010* (MO), *5071* (MO); Barro Colorado I, *McDaniel 5023* (MO); Chagres, *Fendler 275* (BM, F, K, MO); Upper Chilibre River, *Seibert 1504* (MO); Chiva Chiva trail nr Miraflores Lake, *Tyson 1388* (FSU); Fort San Lorenzo, *Burch et al. 1030* (K, MO, NY, UC, US), *Tyson 1577* (FSU), *Tyson & Blum 3702* (MO); Galena Point, *Blum & Dwyer 2144* (MO); Pedro Miguel, *Bro. Heriberto 13* (F). COLÓN: Colón, *Rose 22076* (NY). DARIEN: vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 872* (MO); El Real, *Burch et al. 1052* (F, GH, MO), 2 mi E of Sante Fé, *Tyson et al. 4815* (MO). PANAMA: Cerro Azul at 2000 ft, *Tyson 2058-A* (MO); Canita 18 mi E of Chepo, *Tyson & Smith 4137* (MO); Panama City, *Burch et al. 1417* (MO). SAN BLAS: Soskatupu, *Duke 10181* (MO).

10. **Chamaesyce hyssopifolia** (L.) Small, Jour. N.Y. Bot. Gard. **3:** 429, 1905.

Euphorbia hyssopifolia L., Syst. Nat., ed 10, 1048, 1759.
E. brasiliensis Lam., Encyc. Méth. Bot. **2:** 423, 1788.

Herb, annual or perennating; erect, ascending or decumbent, to 6 dm. *Stem* to 4 mm thick at somewhat woody base, glabrous or sparingly long pilose near base, straw-colored or darker brown. *Leaves* membranous; stipules joined or nearly free at upper nodes, almost obsolete to deltoid, 0.8 mm long, margin short-fringed; blades variable, glabrous or sparsely long pilose, linear-lanceolate, 15-35 × 3-6 mm, the base subcordate, the margin serrate only near the acute apex, to ovate-elliptic, somewhat falcate, 10-30 × 6-10 mm, the base rounded to subcordate, the

margin serrate, the apex obtuse. *Cyathia* terminal and axillary in short-stalked diffuse or compact leafy dichasia, glabrous; glands transversely elliptic or subcircular, the appendages obsolete to prominent, white or pink. *Capsule* glabrous, truncate-cuneiform to broadly ovoid, 1.5-2 mm long, 1.6-1.8 mm wide; seed oblong-ovoid, to 1 mm long, 0.5 mm wide, 4-angled, the faces flat with transverse ridges, brown or black, angles sometimes light.

New World tropics and subtropics and an adventive weed in the Old World. A common weed throughout the Republic, particularly where man's activities have left disturbed ground. This taxon is very variable in other parts of its range but none of the extreme forms which may prove worthy of recognition seem to occur in Panama.

BOCAS DEL TORO: Bocas del Toro I airport, *Lewis et al. 785* (F, GH, MO, NY); vic of Almirante, *Cooper 87* (F), *107* (F); Changuinola, *Lewis et al. 818* (GH, K, MO, UC, US), *Carleton 75* (NY); Changuinola valley, *Dunlap 54* (F); Isla Colón, vic of Chiriquí Lagoon, *von Wedel 2800* (MO, NY), *2954* (F, MO, NY); s. loc., *von Wedel 141* (MO), *183* (MO). CANAL ZONE: Albrook Air Force Base, *Tyson 1104* (MO); vic of Balboa, *Seibert 381* (K, MO, NY); Balboa, *Macbride & Featherstone 36* (F); Barro Colorado I, *Aviles 21* (F), *Bailey & Bailey 155* (F), *155a* (F), *Ebinger 34* (MO), *Hood 1020* (F), *Shattuck 483* (F), *Woodworth & Vestal 409* (F); Chagres, *Fendler 271* (MO), *276* (W), *277* (F, K, MO); Corozal to Pedro Miguel, *Cowell 401* (NY); Culebra I, *Duke 4631* (DAV, MO); ca 1 mi N of Fort Clayton, *Stimson 5193* (DUKE, MO), *5197* (DUKE, MO); Fort Kobbe, *Duke 3952* (MO); Fort Sherman, *Burch et al. 1012* (K, MO, NY, UC); ca 6 mi N Gamboa, *Tyson 1509* (FSU); E of Gatun Locks, *Duke 4301* (DAV); Gatun Sta, *Hayes 675* (NY); Miraflores, *Dwyer 1005* (MO), *White 174* (MO); Santa Rita trail, *Cowell 158* (NY). CHIRIQUÍ: vic of Boquete, *Davidson 601* (F, MO), *Dwyer & Hayden 7615* (MO); David airport, *Lewis et al. 738* (GH, K, MO, NY, UC, US); Río San Pedro, *Dwyer & Hayden 7768* (MO). COCLÉ: betw Porto Posada & Penonomé, *Williams 165* (NY); Río Hato airstrip, *Blum & Dwyer 2481* (MO), *Burch et al. 1155* (F, GH, MO, US). COLÓN: Maria Chiquita, E of Río Piedras, *Dwyer & Kirkbride 7795* (MO); vic of Río Piedras, *Blum et al. 2545* (MO). DARIEN: El Real, *Burch et al. 1051* (GH, MO, UC, US); 0-4 mi up Río Sabana from Santa Fé, *Duke 4168* (MO). HERRERA: rd from La Avena to Pesé, *Burch et al. 1288* (K, MO, NY); ca 10 mi S of Ocú, *Tyson et al. 2864* (MO). LOS SANTOS: ca 3 mi S of Carreta, *Burch et al. 1222* (K, MO, NY); 5-9 mi from Chitré on rd to Las Tablas, *Burch et al. 1221* (MO, UC, US). PANAMA: nr Arraijan, *Woodson et al. 1380* (F, MO, NY); NE of Hacienda La Joya, *Dodge et al. 16905* (MO); Panama Viejo, *Duke 5732* (MO); Panama City, *Duke 4010* (MO); PanAmer Hwy 5-6 mi E of Chepo, *Duke 4021* (DAV, MO); Río Pacora nr confluence with Río Corso, *Duke 12002* (MO). PROVINCE UNKNOWN: s. loc., *Seemann 196* (BM).

36. PEDILANTHUS

Pedilanthus Poiteau, Ann. Mus. Hist. Nat., Paris **19:** 388, 1812, nom. gen. cons.

Shrubs, succulent, becoming woody, usually erect to ascending and only sparsely branched, often somewhat zig-zag, milky latex in all parts. *Leaves* alternate, distichous; short petiolate; stipules small; blades expanded, fleshy, entire, early deciduous. *Cyathia* in axillary or terminal cymes, subtending bracts opposite; involucral bracts 5, partly connate, forming a slipper-shaped structure made up of a widely lobed ventral pair sometimes with glands on the dorsal edges, a basally asymmetric lateral pair with glands on the dorsal edges, and a dorsal bract with glands on each edge. *Staminate flowers* numerous, naked; monandrous; pollen grains ellipsoid, 3-lobed in equatorial view, usually intectate, 3-colporate. *Pistillate*

flower terminal, solitary; naked; ovary 3-celled each with a single ovule, the styles 3, bifid, connate for most of length. *Fruit* a capsule or indehiscent; seed ovoid, smooth or tuberculate, ecarunculate.

A tropical American genus of 14 species centered in Mexico. Only a single species is represented in Panama, and all collections (at least from naturally occurring plants), fall in the typical subspecies. The genus has been monographed by Dressler (Contr. Gray Harb., Harv. Univ. **182:** 1-188, 1957), who treats exhaustively the variants that may be found as cultivated plants or escapes.

1. **Pedilanthus tithymaloides** (L.) Poiteau, Ann. Mus. Hist. Nat., Paris **19:** 390, 1812, subsp. **tithymaloides.**

Shrub to 1.5 m, branches terete, puberulent but soon glabrate, often leafless. *Leaves* somewhat succulent; stipules blunt, dark brown; petiole 3-8 mm long; blade elliptic-ovate, 6-10 × 2-4 cm, the base cuneate, the apex acute or somewhat attenuate; sparsely puberulent above, more densely so below. *Cymes* condensed, the subtending bracts flushed red, puberulent; involucre to 14 mm long, the bracts green at base, deep red above, puberulent within, glabrous without. *Capsule* ovoid, to 6 mm long, 7 mm diam, glabrous; seed ovoid, obscurely angled, to 5 mm long, the surface smooth, gray.

This is the most widely ranging species of the genus and this subspecies alone spans the mainland area from Mexico to northern South America. In Panama it is most common at medium elevations, but it (and possibly some distinct cultivars) may frequently be seen as low hedges in most provinces.

CANAL ZONE: Tabernilla, *Cowell 276* (NY). COCLÉ: Aguadulce, *Pittier 5000* (US); La Pintada, *Hunter & Allen 514* (MO); Penonomé, *Williams 229* (NY, US). HERRERA: vic of Ocú, *Stern et al. 1737* (MO). PANAMA: Alahuela, nr Madden Dam, *Dodge et al. 16824* (GH, MO, S); Taboga I, *Macbride 2804* (F, US). VERAGUAS: Canazas, *Tyson 3622* (MO); headwaters of Río Canazas, *Allen 196* (F, MO).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 101. ANACARDIACEAE[1]

BY WILL H. BLACKWELL, JR. AND CALAWAY H. DODSON
Missouri Botanical Garden, St. Louis, Missouri and
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Trees or shrubs with resinous bark. *Leaves* alternate, estipulate, imparipinnately compound, less frequently trifoliolate or simple. *Inflorescences* paniculate, terminal or axillary, often with numerous flowers. *Flowers* small, actinomorphic, ☿ or ♂♀ by reduction; sepals usually 4-5, free or variously connate; petals distinct, typically 4-5, infrequently absent; stamens 5-10(-12), all fertile or occasionally some or most reduced and sterile, the introrse anthers 2-celled and longitudinally dehiscent; disc or nectariferous cushions usually present and intrastaminal, rarely extrastaminal or absent; pistil 1, the ovary superior, (1-)3(-5)-carpellate, 1-locular (rarely 2-5-locular), the ovule solitary (the ovary occasionally with 3 ovules only one of which is functional) and anatropous, the placenta apical, basal or less frequently lateral, the styles 1-5, terminal or excentric, the stigmas typically as many as the carpels. *Fruit* drupaceous or less frequently nut-like, most often dry but occasionally with a fleshy mesocarp; seed solitary, the embryo curved, the endosperm sparse or absent.

A family of 73 genera and about 600 species, chiefly tropical but extending into southern Europe and temperate Asia and America. Ten genera are known to occur in Panama[2]; eight are native and two are introduced and probably naturalized.

Several members of the family have considerable economic value; a number produce poisonous effluvia responsible for dermatitis in persons allergic to these secretions.

a. Leaves simple, entire.
   b. Disc extrastaminal; stamens 5; leaf-blades usually acuminate or acute at the apex ..... 1. *Mangifera*
   bb. Disc intrastaminal or absent; stamens 7-12; leaf-blades obtuse to rounded or emarginate at the apex.

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2] Standley (Contr. U. S. Nat. Herb. **27**: 241, 1928) reported that trees of *Semecarpus anacardium* L. f. were planted at Ancon. The genus *Semecarpus* is not included in this treatment as there is no evidence of its spread in Panama, either by naturalization or cultivation.

c. Inflorescences paniculate; flowers 5-merous; stamens basally connate; disc lacking; ovule lateral; fruit a reniform nut borne on an accrescent, fleshy pedicel (the hypocarp) .....2. *Anacardium*

cc. Inflorescences virtually spicate; flowers 4-merous in Panamanian representatives; stamens free; intrastaminal disc present; ovule apical; fruit an ovoid drupe, the subtending pedicel not accrescent .....3. *Campnosperma*

aa. Leaves compound (rarely with simple and compound leaves on the same plant).

d. Stamens 10, twice the number of petals.

e. Styles 4-5 (if 3, then the flowers red and the inflorescences arising laterally on old wood).

f. Ovary and styles pubescent; ovary 1-locular; well-developed stamens and pistil not present in the same flower; petals not uncinate at the tip; leaflets opposite or subopposite .....4. *Tapirira*

ff. Ovary and styles glabrous; ovary 3 to 5-locular; well-developed stamens and pistil occurring in the same flower; petals uncinate at the tip; leaflets frequently both opposite and alternate (often on the same leaf) .....5. *Spondias*

ee. Styles 3 or single with a 3-lobed stigma.

g. Drupes oblique and strongly compressed, the exocarp and mesocarp not separating; calyx cupular, the lobes shallow; petals acute or subacuminate; stamens and pistil well-developed in the same flower; leaflets petiolulate .....6. *Mauria*

gg. Drupes neither oblique nor appreciably compressed, the exocarp deciduous; sepals free or connate only at the base; petals obtuse, rounded or truncate; stamens and pistil not well-developed in the same flower; leaflets sessile or subsessile (rarely with petiolules to 1 mm long) .....7. *Schinus*

dd. Stamens 5, equal in number to the petals.

h. Ovule subapical; the 3 styles separate to the ovary; calyx-lobes strikingly accrescent in fruit; fruit 3-5 times longer than broad; flowers pedicillate; a pistillode not present in ♂ flowers .....8. *Astronium*

hh. Ovule basal or affixed laterally near the base; style single or 3-parted only at the apex; calyx-lobes not accrescent in fruit; fruit not more than 1½ times longer than broad; flowers pedicillate or sessile, ☿ or functionally ♂ flowers with a pistillode.

i. Flowers sessile, each subtended by 3 persistent deltoid bracts; ovule attached laterally near the base; drupes red, the exocarp and mesocarp not separating; inflorescences not densely flowered; seed occupying a relatively small portion of the drupe lumen .....9. *Mosquitoxylum*

ii. Flowers with pedicels 1-4.5 mm long, not subtended by 3 persistent deltoid bracts; ovule basal; drupes white, the exocarp deciduous, the mesocarp waxy and with conspicuous dark streaks; inflorescences densely flowered; seed occupying the entire drupe lumen ....10. *Toxicodendron*

1. MANGIFERA

Mangifera L., Sp. Pl. 200, 1753; Gen. Pl. ed. 5, 93, 1754.

Trees, often attaining great size. *Leaves* petiolate, the blades simple and entire. *Panicles* terminal, large, the bracts deciduous. *Flowers* ☿, the pedicels articulated; calyx-lobes 4-5, imbricate, deciduous; petals 4-5, free or adnate to the disc, imbricate, the nerves often ridged ventrally; stamens usually 5 (rarely 10-12), with 1 fertile and much larger than the rest (rarely with 2, 3 or all 5 fertile);

Fig. 1. *Mangifera indica* L.: A, habit (×½); B, flower (ca ×10). A after *White* 282 (MO); B after *Lewis et al.* 696 (MO).

disc extrastaminal, 4-5-lobed, tumid or less frequently much reduced; ovary 1-carpellate, 1-locular, the solitary ovule affixed just above the base of the locule, the style excentric. *Fruit* a fleshy drupe with a large, compressed seed.

A genus of about 53 species indigenous to tropical and subtropical Asia; one species is cultivated throughout the tropics of the Old and New World (including Panama) for its edible fruit.

Useful reference:

Mukherji, S., A monograph on the genus *Mangifera* L. Lloydia **12:** 73-136, 1949.

1. **Mangifera indica** L., Sp. Pl. 200, 1753.—Fig 1.

Tree 5-40 m high, the branches glabrous. *Leaves* with petioles 0.8-6.2 cm long; blades oblong-lanceolate to oblong or narrowly elliptic-lanceolate, apically acuminate or acute (rarely obtuse), basally cuneate to narrowly obtuse, 9-36 cm long, 2-7 cm broad, subcoriaceous or coriaceous, marginally straight or subundulate, glabrous on both surfaces, often glossy above and with prominulous or prominent reticulation. *Panicles* 15-50 cm long, densely flowered, pyramidal, the branches irregularly pilosulous and often spreading. *Flowers* 5-merous, the pedicels 0.5-4(-6) mm long; calyx-segments ovate-lanceolate, concave, 1.5-3 mm long, externally pubescent, spreading but arcuate and the distil portion ascending; petals oblanceolate or obovate to oblong, acute to obtuse or rounded, plicate toward the base, each producing a ventro-basal flap of tissue extending between the lobes of the disc, yellow or cream or pink (the ventral ridges often dark-red or rose-colored and imparting a streaked appearance to the corolla), 3-5 mm long, spreading or somewhat ascending, strongly recurved at the tip; disc consisting of 5 separate (sometimes apically coalescent) tumid cushions in a whorl between the stamens and petals and alternate with the petals; stamens 5, 1 large and fertile, the rest reduced to staminodes; ovary obliquely subglobose or ovoid, the style slender, often subequal in length to the fertile stamen. *Drupes* large (from 6 cm), often oblong or subreniform, frequently yellow externally (varying from yellow to green or apricot), the mesocarp thick and juicy, often orange or yellow in color.

Although a native of the Indian Peninsula, the mango is cultivated throughout Latin America (also in southern Florida and southern California) as well as the tropics of the Old World. In many regions (as in Panama) it has becomes a significant naturalized element of the flora.

CANAL ZONE: Gatun, *Hayes 4* (US); in Government forest along Las Cruces Trail, *Hunter & Allen 686* (MO), *758* (MO); Barro Colorado I, *Shattuck 96* (F, MO), *Wetmore & Abbe 94* (F); along the old Las Cruces Trail, betw Fort Clayton & Corozal, *Standley 29171* (US); Obispo, *Standley 31757* (US); vic of Miraflores Lake, Cocoli I, *White 282* (MO, US), *283* (MO), *284* (MO), *285* (MO), *286* (MO), *287* (MO), *288* (MO), *291* (MO), *292* (MO, US), *293* (MO); s. loc., *Epplesheimer s.n.* (F), *White 253* (MO), *349* (MO), *350* (MO), *351* (MO, US), *352* (MO). CHIRIQUÍ: 12.4 mi N of David, *Lewis et al. 696* (MO). LOS SANTOS: Bahia Honda, *Elmore H13* (F, US). PANAMA: Taboga I, *Allen 132* (MO).

Although several different parts of the mango are utilized in various regions of the world (young leaves, seeds, bark, flowers, etc.), it is the edible fruit which is most sought after. The mango fruit ranks among the leading fruit corps of the world as a whole, furnishing fruit to about ⅕ of the earth's inhabitants (Barkley, Missouri Bot. Gard. Bull. **24:** 218, 1936). The fruit is eaten raw and used in the preparation of preserves, jellies, tarts, sauces, and chutneys. Good varieties are scarce in many parts of Latin America as little selection is practiced.

2. ANACARDIUM

Anacardium L., Sp. Pl. 383, 1753; Gen. Pl. ed. 5, 180, 1754.

Rhinocarpus Bertero & Balbis ex H.B.K., Nov. Gen. Sp. Pl. **7:** 5, 1824.

Trees or shrubs, evergreen. *Leaves* short-petiolate; blades simple, entire, coriaceous. *Panicles* large, terminal. *Flowers* small, ☿, bracteate, the pedicels accrescent in fruit; calyx 5-parted, the segments imbricate in bud; petals 5, recurved, imbricate in bud; stamens (7-)10(-12), unequal, all or a few or only 1 fertile, the filaments basally connate and adnate to the torus; disc or nectariferous outgrowths lacking; ovary subglobose to turbinate or obovate, somewhat gibbous, 1-celled, 1-ovulate, the ovule lateral, ascending on a very short funicle, the style compressed-conic, excentric, as long or slightly longer than the ovary. *Nut* rather large, reniform, laterally compressed, virtually filled by the solitary reniform seed, borne at the apex of a fleshy hypocarp (the accrescent pedicel).

A genus of eight or nine species native to tropical America; only two species occur in Central America, including Panama.

a. Tree 20-37 m high; leaf-blades 14-31 cm long; panicles with brown pubescence; 4 stamens much longer than the rest; staminal filaments pubescent (except the extreme distal portion); hypocarp 2-3 mm broad when ripe .....1. *A. excelsum*

aa. Tree seldom reaching 10 m in height; leaf-blades 6-15.5 cm long; panicles with gray pubescence; 1 stamen much longer than the rest; staminal filaments entirely glabrous; hypocarp much broader than 3 mm when ripe .....2. *A. occidentale*

1. **Anacardium excelsum** (Bertero & Balbis) Skeels, U.S. Bur. Pl. Ind. Bull. **242:** 36, 1912.

Rhinocarpus excelsa Bertero & Balbis ex H.B.K., Nov. Gen. Sp. Pl. **7:** 6, *t. 601,* 1824 (incl. *Anacardium ? rhinocarpus* DC., Prodr. **2:** 62, 1825).

Tree 20-37 m high. *Leaves* aggregated toward the branch-tips, the petioles 7-21 mm long; blades usually obovate or broadly oblanceolate, less frequently oblong or ± elliptic, apically obtuse to rounded or slightly emarginate, basally cuneate and symmetric or asymmetric, glabrous or essentially so, 14-31 cm long, 5-12 cm broad, with prominulous to prominent reticulation on both surfaces. *Panicles* 15-35 cm long, with a brown or rufescent pubescence, the bracts reduced, 1-2.5 mm long. *Flowers* with pedicels 1-6 mm long; calyx-segments ovate, 1-3 mm long, crassulate except at the margins; petals linear-oblong, 3-6 mm long, 1-1.75 mm broad, cream or green, ± adnate to the stamen-tube; stamens (7-)10(-12),

4 much longer than the rest and extending well beyond the point at which the petals become recurved, the filaments subulate, rather conspicuously pubescent except on the extreme distal portion; ovary 0.2-0.5 mm long. *Hypocarp* 5-20 mm long, thickening to a breadth of 2-3 mm, twisted or sigmoid. *Nut* 2.5-3.5 cm long when ripe, 1-2 cm broad.

Costa Rica, Panama and northern South America.

BOCAS DEL TORO: s. loc., *Cox 18823* (US). CANAL ZONE: Barro Colorado I, *Aviles 986* (F), *Brown 70* (F), *Carpenter 2* (F), *Frost 118* (F), *Kenoyer 651* (US), *Knight 10* (F), *Shattuck 802* (F, MO, US), *Wetmore & Abbe 194* (F), *199* (F), *Wilson 5* (F), *Woodworth & Vestal 337* (F); Albrook, U.S. Army Tropic Test Center Site, *Dwyer & Robyns 50* (MO); nr Santiago, *Harvey 5270* (F); river bank nr Gatun, *Pease 22880* (US); Corozal, *Piper 5297* (US); around Bohio, *Pittier 3419* (US); nr Fort Randolph, *Standley 28704* (US); vic of Fort Sherman, *Standley 30929* (US); Obispo, *Standley 31740* (US); Curundu on rd past Survival School, *Tyson 3476* (MO). CHIRIQUÍ: Progreso, *Cooper & Slater 206* (F). COCLÉ: Penonomé & vic, *Williams 291* (US). DARIEN: trail betw Pinogana & Yavisa, *Allen 297* (MO, US); vic of Pinogana, *Allen 4286* (MO); Pico Piriaque, *Duke 8146* (MO). HERRERA: vic of Ocú, *Allen 4075* (MO). PANAMA: Río Las Lajas, *Allen 1605* (F, MO, US): vic of Bejuco, *Allen 4296* (MO); Río Indio drainage, ca 9 mi E of Trans-Isthmian Hwy, *Barbour 1057* (F); San José I, Red Hill Grade, *Johnston 649* (MO, US); Bella Vista, *Macbride 2729* (F, MO, US); Sabanas, *Bro. Paul 301* (US); nr the big swamp E of Río Tocumen, *Standley 26576* (US); Río Tocumen, *Standley 26743* (US), *26746* (US); Río Tapía, *Standley 28270* (US). VERAGUAS: vic of Santa Fé, Río Santa María, *Allen 4424* (MO).

This species, known as *espavé* or *espavel*, is a large forest tree of rather common occurrence in Panama. The wood is reportedly used in making trays and canoes and the bark for poisoning fish. The hypocarp is edible but the tree is not cultivated and has not been appreciably exploited economically.

2. **Anacardium occidentale** L., Sp. Pl. 383, 1753.—Fig. 2.

Tree to 8(-10) m. *Leaves* ± aggregated toward the apex of the branchlets, the petioles 5-20 mm long; blades broadly oblong-ovate to somewhat obovate, obtuse to rounded or slightly emarginate at the apex, cuneate to obtuse or rounded at the base, glabrous, 6-15.5 cm long, 3.5-9 cm broad, with prominulous reticulation on both surfaces. *Panicles* 7-16.5 cm long, with gray pubescence; bracts usually at least sparsely puberulent, those subtending the lower primary branches of the panicle oblanceolate or oblong and foliaceous (though much reduced in size), those subtending the distal branches and flowers or flower-groups ovate and resembling the calyx-lobes. *Flowers* with pedicels 0.5-7 mm long; calyx-segments lanceolate to lance-ovate, 2.5-5 mm long, 1-2.3 mm broad, moderately grayish-appressed-puberulent dorsally; petals linear to linear-lanceolate or narrowly linear-elliptic, 6-13 mm long, 1-2 mm broad, greenish-yellow with red streaks at anthesis, turning dark red with age; stamens 10, 1 much longer than the others and extending well beyond the point at which the petals become recurved, the filaments glabrous; ovary 0.2-0.5 mm long. *Hypocarp* red or yellow at maturity, to 10 cm long and 5 cm broad, ± obovate. *Nut* gray, 2-3.2 cm long, 1-2 cm broad.

Present and often common by introduction and cultivation throughout the tropics of the New and Old World, becoming naturalized in many places; probably native from Costa Rica to Brazil and Ecuador.

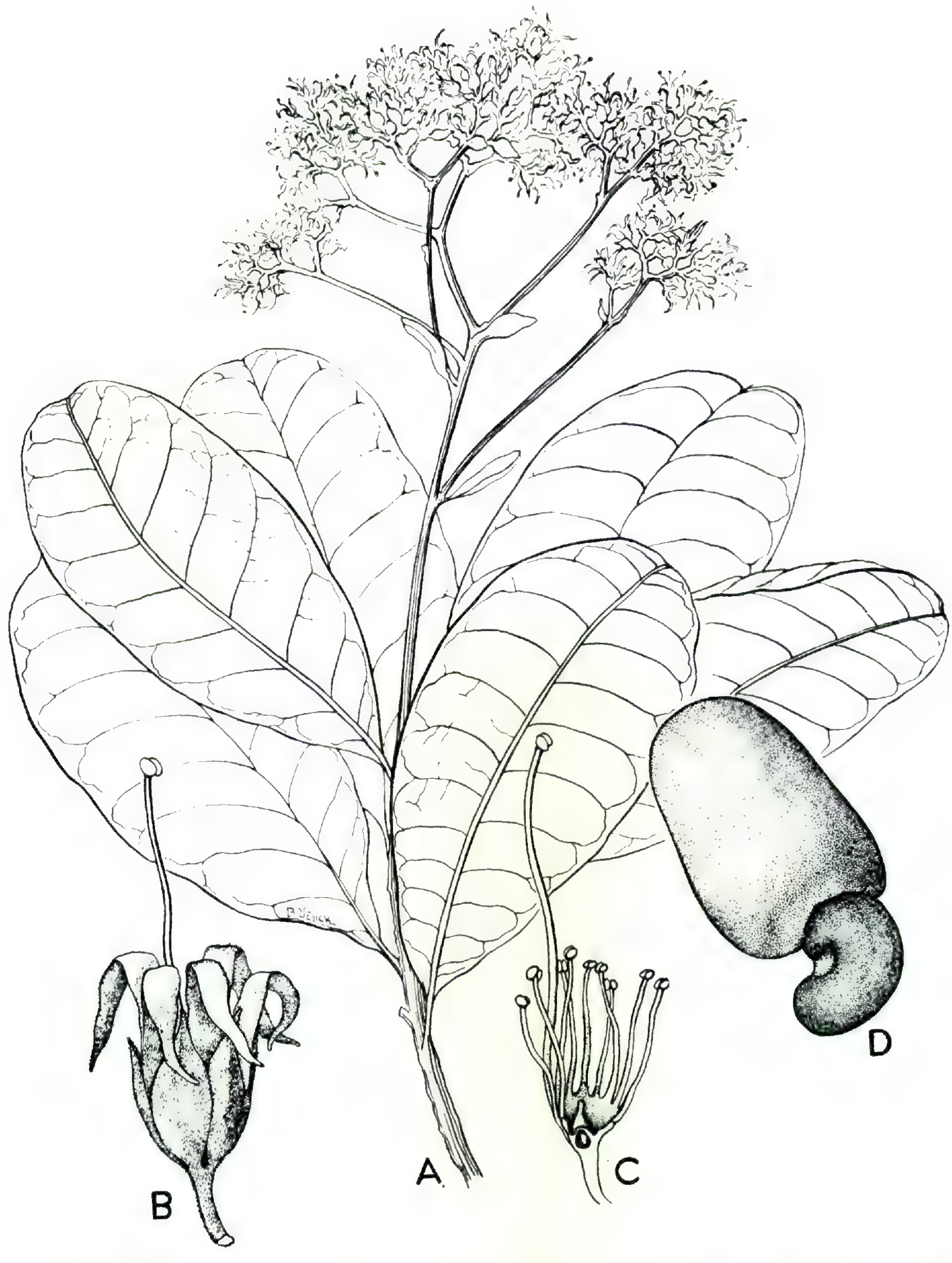

Fig. 2. *Anacardium occidentale* L.: A, habit (×½); B, flower (×4); C, id., calyx and corolla removed (×4); D, nut and hypocarp (×⅔). A, leaves after *Allen 1079* (MO), inflorescence after *Macbride 2728* (MO); B-C after *Macbride 2728* (MO); D after *Blum 2224* (MO).

CANAL ZONE: s. loc., *Blum 2224* (MO); [Las Sabanas?], *Bro. Celestine 105* (US); betw Mt Hope & Santa Rita Trail, *Cowell 92* (US); Barro Colorado I, *Epplesheimer 2* (F), *Wilson 82* (F), *Woodworth & Vestal 711* (F); s. loc., *Epplesheimer s.n.* (F); Chagres, *Fendler 308* (MO, US); Gatun, *Hayes 9* (MO, US); nr Fort Randolph, *Maxon & Harvey 6522* (US); [Sabanas?], *Bro. Paul 209* (US); betw Corozal & Ancon, *Pittier 2633* (US); Balboa, *Standley 25510* (US), *27127* (US); Curundu, *Tyson 3574* (MO); Ancon Hill *Williams 36* (US). CHIRIQUÍ: 25 mi E of David, *Harvey 2568* (F); 12.4 mi N of David, *Lewis et. al. 719* (MO). COCLÉ: Aguadulce, *Pittier 4845* (US). COLÓN: betw France Field, Canal Zone & Cativa1, *Standley 30324* (US). DARIEN: vic of El Real, Río Tuira, *Stern et al. 791* (MO, US). HERRERA: vic of Ocú, *Allen 4063* (MO). PANAMA: Taboga I, *Allen 130* (F, MO), *Hjerting & Rahn 615* (US); 1 mi E of Tocumen airport on side rd off Inter-Amer Hwy, *Blum & Tyson 1964* (MO); along rd betw Panama & Chepo, *Dodge et al. 16706* (MO); Capira, *Duke 6031* (MO); Cermeño, *Dwyer & Robyns 109* (MO); on sabanas, rd to Chepo, *Hunter & Steyermark s.n.* (MO); Chorrera, *Killip 3404* (US); Bellavista, *Macbride 2728* (F, MO, US); nr Tapia River, Juan Díaz region, *Maxon & Harvey 6720* (US); Tumba Muerto Rd, nr Panama, *Standley 29829* (US). VERAGUAS: vic of Santiago, *Allen 1079* (MO); rd betw San Francisco & Santa Fé, *Stern et al. 1918* (MO).

This species is commonly known as *marañón* and *jocote marañón* in Central America. It produces the commercially important cashew nut. The cashew nut must be roasted before the seed, the "cashew nut" of commerce can be eaten. Cashew nuts are not produced on a large economic scale in tropical America (the native home of the cashew) but are largely exported from India where the cashew is extensively cultivated. The ripe, red or yellow hypocarp (the swollen pedicel subtending the nut) has a juicy, spongy, yellowish flesh and is used as a fruit in tropical America. The hypocarp is often mistaken for the true fruit and is sometimes referred to as the "cashew apple." Care should be exerted to avoid the nut when eating the hypocarp as the unroasted pericarp contains a volatile, irritating oil which may blister the skin.

3. CAMPNOSPERMA

Campnosperma Thwaites, Hook. Jour. Bot. Kew Gard. Misc. **6:** 65, 1854, nom. gen. conserv.

Cyrtospermum Bentham, loc. cit. **4:** 13, 1852, non *Cyrtosperma* Griffith (Notul. Pl. Asiat. **3:** 149, 1851).

Drepanospermum Bentham in Bentham & Hooker f., Gen. Pl. **1:** 425, 1862.

Trees. Leaves petiolate or subsessile, clustered toward the branch-tips; blades simple, entire, coriaceous. *Inflorescences* paniculate, large, axillary but arising from the distal nodes of a branch. *Flowers* polygamo-dioecious, 3-5-merous; calyx persistent, the lobes imbricate in bud; petals erect or spreading, imbricate at anthesis; stamens 6-10, free, inserted at the base of the disc, subequal or slightly unequal, incurved, the filaments flattened, slightly narrowed toward the apex; intrastaminal disc fleshy, annular, entire or crenate-sulcate; ovary 1-2-locular, the style short, the stigma lobate-discoid, the ovule apical or basal. *Drupes* ovoid, erect, fleshy, 1-locular or 2-locular (one empty).

The genus is primarily East Indian. Two species occur in the New World tropics, one being native to Panama.

1. **Campnosperma panamensis** Standley, Jour. Arnold Arb. **2:** 111, 1920.—Fig. 3.

Tree of large to medium size, the thick branches often with rugose and scaly bark, the young parts stellate-puberulent. *Leaves* short-petiolate or subsessile, ascending; blades oblong-obovate, rounded to emarginate at the apex, basally equilateral and cuneate to attenuate, stellate-pubescent beneath and also lepidote with minute brown scales, glabrous above and with scattered scales, somewhat lustrous above, 14-35 cm long, 5.5-15 cm broad, the midvein conspicuously raised beneath, the 32-52 ± parallel secondaries pinnate, the reticulation prominulous below and prominent above. *Panicles* to 40 cm long, spicate, often with several primary branches arising from the main axis, with a brown stellate pubescence, occasionally with small ovate or lance-ovate bracts subtending the branches. *Flowers* with pedicels 0-2 mm long; calyx-lobes 4, broadly ovate, ca 0.5 mm long, stellate-pubescent; petals 4, ovate, broadly acute to rounded, 1.2-2 mm long, concave, glabrous, yellow; stamens 8, equal to or slightly shorter than the petals; disc tumid and conspicuous, crenate; ovary lepidote, latissimus-ovate, 1-locular, the ovule apical. *Drupes* triangular-ovoid, 1-1.5 cm long.

Costa Rica and Panama, infrequent.

BOCAS DEL TORO: Chiriquicito Lagoon, *Little s.n.* (holotype A; isotype US); swamp nr Almirante, *Rowlee & Stork 1001* (US); Laguna de Chiriquí, *Stern & Chambers 107* (A, F, MO, US). PROVINCE UNKNOWN: s. loc., *Cooper & Slater 154* (F, GH, US).

Commonly known as *orey*.

4. TAPIRIRA

Tapirira Aublet, Hist. Pl. Gui. Fr. 470, 1775.

Trees or shrubs, erect or subscandent, glabrous or pubescent. *Leaves* imparipinnate, the leaflets entire or serrate. *Panicles* axillary or terminal. *Flowers* polygamodioecious, small, frequently greenish-yellow and fragrant; calyx-segments 5, imbricate, persistent; petals 5, spreading, imbricate in bud; stamens 10, inserted below the disc, the anthers ovate to ± globose; disc intrastaminal, 5-10-lobed; ovary ovoid, 1-locular, the ovule apical, the styles 4-5, short, conic, the stigmas simple. Drupes ± oblique-oblong, fleshy, the stone rugulose-crustaceous; seed solitary, oblong, the testa thinly membranaceous.

The genus *Tapirira* is much in need of monographic attention. The exact number of valid species is undetermined but probably does not exceed 15. Asian, African and Tropical American representatives are known; two species occur in Panama. This genus is easily confused with *Protium* in the *Burseraceae*, particularly when specimens lack flowers. *Tapirira chagrensis* Pittier (type from Chagres River above Alhajuela, Province of Panama, US) is *Protium sessiliflorum* (Rose) Standley.

a. Inflorescences paniculate, often possessing secondary and tertiary branches, densely-flowered; flowers often appearing clustered, the pedicels 1-3 mm long; drupes 0.5-1.5 cm long ..... 1. *T. guianensis*

aa. Inflorescences paniculate-spicate, simple or the rachis with only primary branches, rather sparsely flowered; flowers never clustered, the pedicels less than 0.5 mm long; drupes 1.7-2.7 cm long ..... 2. *T. brenesii*

Fig. 3. *Campnosperma panamensis* Standley: A, habit (×⅓); B, flower (×7); C, id., longitudinal section (×7). After *Stern & Chambers 107* (MO).

1. **Tapirira guianensis** Aublet, Hist. Pl. Gui. Fr. 470, *t. 188*, 1775.—Fig. 4.

T. myriantha Triana & Planchon, Ann. Sci. Nat., Bot., sér. 5, **14:** 295, 1872.

Tree 3-40 m high; branches developing gray bark, the young portions dotted with lenticels. *Leaves* clustered toward the branch-tips, with (1-)2-5(-7) pairs of leaflets, the rachis 5-35 cm long and minutely ferruginous-puberulent or glabrous, the leaflets opposite, with petiolules 2-11 mm long (not including the petiolule of the terminal leaflet which is often longer); lamina of leaflets oblong or oblong-lanceolate to somewhat obovate or ovate, slightly oblique, acuminate or subacuminate apically (the acumen rounded or emarginate), rarely rounded or emarginate at the apex, basally cuneate to broadly obtuse and often somewhat assymetric, 5-20 cm long, 1.5-8 cm broad, glabrous or sparsely puberulent beneath (rarely above) along the main veins, membranous or slightly coriaceous, entire, paler beneath, often lustrous above, the secondary veins brochidodrome. *Panicles* axillary but arising from the distal nodes of a branch, densely-flowered, 8-37 cm long, the branches at least sparsely ferruginous-puberulent (the trichomes ascending or appressed). *Flowers* functionally ♂ ♀ (one sex well developed morphologically and the other ± vestigial), occasionally ☿, the pedicels 1-3 mm long, 0.2-0.5 mm broad (in flower), rather conspicuously hirtellous with ascending to appressed trichomes (rarely glabrate); calyx-segments deltoid to rotund-ovate, apically acute to rounded, sparsely appressed-hirtellous externally, 0.5-0.75 mm long; petals elliptic or oblong-elliptic to ovate-lanceolate or subovate, acute to obtuse or rounded, occasionally slightly erose-dentate apically, 1.5-2.5 mm long, ascending to spreading or reflexed, yellowish-white or greenish-white; stamens 10, 1.5-2.5 mm long (hypoplastic in functionally ♀ flowers), the filaments rather slender, the anthers ovate, basally cordate or auriculate, 0.3-0.5 mm long; disc 10-crenulate occasionally tumid and subentire; ovary 1-1.5 mm long and oblong-ovoid to ovoid or slightly obovoid in functionally ♀ flowers, rather sparsely puberulent, greatly reduced and concealed by the disc in functionally ♂ flowers, the styles 5 (rarely 4 in functionally ♂ flowers), free and well spaced in functionally ♀ flowers, connivent and free or lightly coalescent basally in functionally ♂ flowers, stubby, 0.1-0.5 mm long, conspicuously pubescent, each surmounted by a slightly enlarged disciform stigma. *Drupes* ovoid to oblong or obovoid, 0.5-1.5 cm long, often showing remnants of the styles; seed pendulous from the locule apex or virtually so.

Panama to Peru, Brazil and Paraguay.

COLÓN: Loma de la Gloria, nr Fató (Nombre de Dios), *Pittier 4101* (F, US).

Collections of *T. myriantha* and *T. guianensis* from northern South America (deposited in MO) were compared and were found to be morphologically similar.

2. **Tapirira brenesii** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 628, 1937.

Tree 8-20 m high; branches brown or gray, subterete, lenticellous, often strigulose, glabrous or sparsely appressed-puberulent. *Leaves* with 2-5 pairs of opposite leaflets, the rachis 5-27 cm long and often striolate, the leaflets with petiolules 2-10 mm

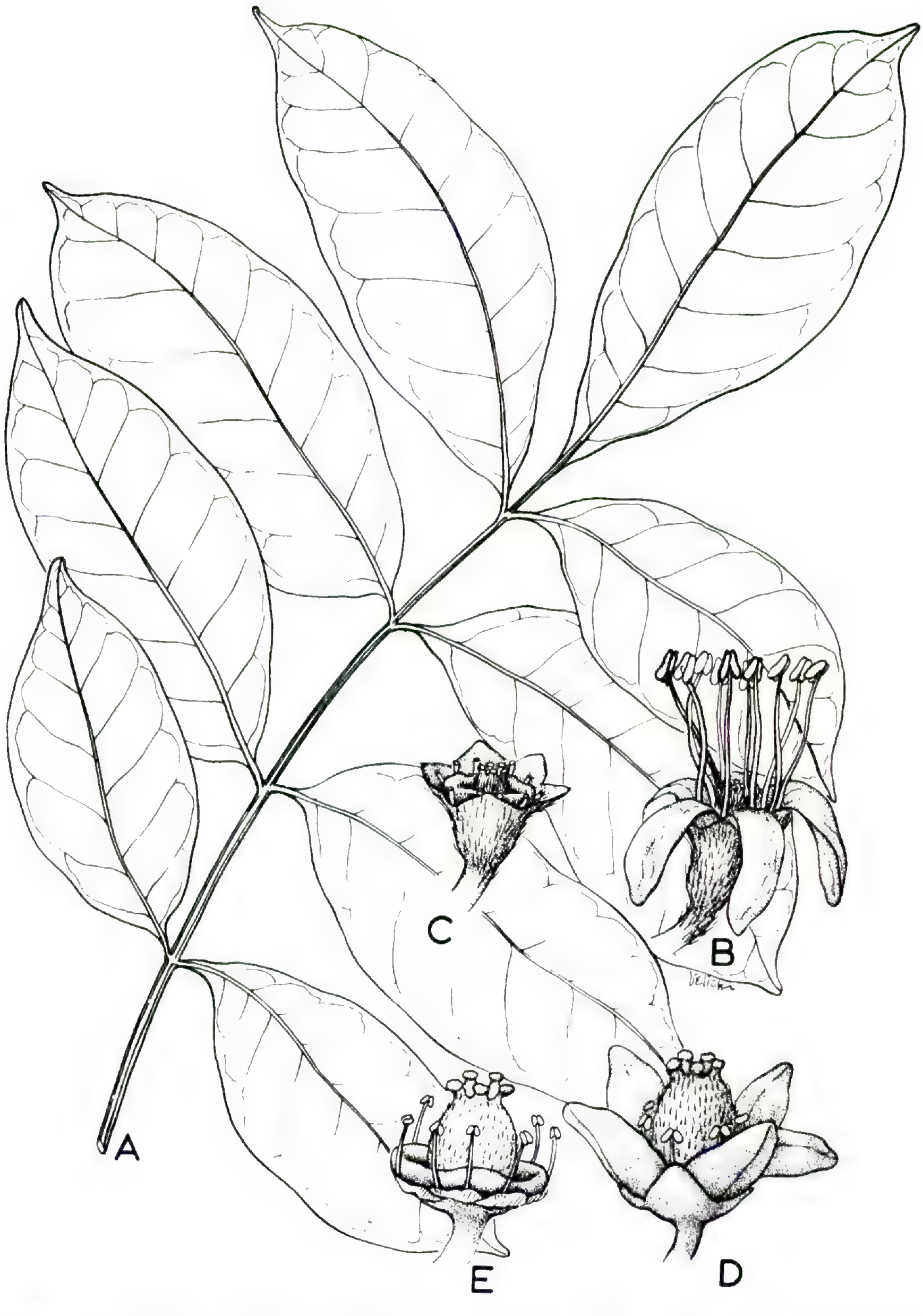

Fig. 4. *Tapirira guianensis* Aublet: A, compound leaf (×⅔); B, functionally ♂ flower (×10½); C, id., petals and stamens removed (×10½); D, functionally ♀ flower (×9½); E, id., calyx and corolla removed (×9½). A after *Hassler 7771* (MO), Paraguay; B-C after *De La Cruz 4604* (MO), British Guiana; D-E after *De La Cruz 4436* (MO), British Guiana.

long; lamina of leaflets oblong-lanceolate to ovate-lanceolate or elliptic, apically acuminate or subacuminate (the acumen obtuse to rounded or emarginate), obliquely cuneate to obtuse at the base, 5.5-13.5 cm long, 2-5 cm broad, entire, coriaceous or subcoriaceous, glabrous or lightly appressed-pilose on the main veins beneath, the reticulation prominulous. *Panicles* axillary to the upper leaves, rather sparsely flowered, 4-16.5 cm long, appressed-hirtellous with ferruginous trichomes, spicate, with primary branches or simple. *Flowers* functionally ♂ ♀, sessile or with pedicels less than 0.5 mm long; calyx-segments sparsely appressed-hirtellous or glabrate, rotund-ovate, ca 1 mm long; petals white, oblong or slightly obovate, 1.8-3.5 mm long, often spreading or reflexed; stamens 1-2 mm long, reduced to staminodes in ♀ flowers; disc 10-crenulate; ovary oblong, ca 1.5 mm long in ♀ flowers, rather sparsely appressed-hirtellous, reduced to a pubescent pistillode in ♂ flowers, the styles ca 0.2 mm long, each surmounted by a slightly expanded stigmatic region. *Drupes* ovoid to oblong, reddish-purple, 1.7-2.7 cm long, carnose.

Nicaragua, Costa Rica and Panama.

CHIRIQUÍ: Boquete Distr, *Davidson 850* (F, US).

It is difficult to separate specimens of this species which do not have mature flower from *Protium sessiliflorum* (Rose) Standley of the *Burseraceae*.

5. SPONDIAS

Spondias L., Sp. Pl. 371, 1753; Gen. Pl. ed. 5, 174, 1754.

Warmingia Engler in Martius, Fl. Bras. **12**(2): 281, 1874.

Shrubs to large trees. *Leaves* odd-pinnate, often crowded toward the branch apex, deciduous, the leaflets alternate or opposite, membranous or subcoriaceous, petiolulate or rarely subsessile. *Inflorescences* paniculate to racemose or subcapitate, terminal or lateral, large or small. *Flowers* small, ☿ or less often ♂ ♀, pedicellate or sessile; calyx-segment (4)5, small, deciduous, slightly imbricate; petals (4)5, erect to spreading or reflexed, subvalvate in bud; disc intrastaminal, cupular, crenate; stamens (4-)8-10, inserted below the disc; ovary 3-5-locular, the styles 3-5, connivent above but free (rarely united by their stigmas), a distinct stigmatic region apparent or not, the ovules solitary in each locule, apical. *Fruit* a fleshy drupe, 1-5-locular; seeds with a membranous testa.

A genus of about eight species, the majority of Asian distribution; two species occur in Central America including Panama.

a. Shrub or small tree; lamina of leaflets usually less than 6 cm in length; inflorescences lateral on older (leafless) branches, racemose-panicuate to subcapitate, 0.5-8 cm long; petals erect or ascending strictly, red; styles (3)4, each constricted strongly at the junction with its capitate stigma; mature fruits red or purple ..... 1. *S. purpurea*

aa. Small to large tree; lamina of leaflets usually 6 cm or more in length; inflorescences terminal on leafy branches of the season, paniculate, 15-40 cm long; petals spreading or reflexed, white or yellow; styles 5, not appreciably constricted at the beginning of the stigmatic portion; mature fruits yellow ..... 2. *S. mombin*

1. **Spondias purpurea** L., Sp. Pl. ed. 2, 613, 1762.—Fig. 5(E).

S. cytherea Sonn., Voy. Ind. Or. Chin., *t. 123*, 1782.
Warmingia pauciflora Engler in Martius, Fl. Bras. **12**(2): 281, *t.* 57, 1874.
Spondias purpurea var. *venulosa* Engler in Martius, loc. cit. 373, 1876.
S. macrocarpa Engler in Martius, loc. cit. 375, *t.* 78.
S. purpurea var. *munita* Johnston, Sargentia **8**: 182, 1949.

Shrub or small tree to 10(-15) m high with smooth gray bark, the branches stout. *Leaves* with (3-)5-12 pairs of leaflets, the rachis 5-25 cm long (often sulcate or bisulcate above and with pilose trichomes bordering the grooves), the leaflets alternate or opposite, with petiolules 0.5-3 mm long and frequently pilose; lamina of leaflets obliquely elliptic to obovate or less often ovate, apically acute or subacuminate to rounded or emarginate and often cuspidate, basally typically acute but varying from subattenuate to obtuse, assymetric at the base, entire or serrate (the teeth sometimes with a cilium at the tip), 1.5-6 cm long, 0.7-3 cm broad, membranous, pilose along the midvein (and sometimes on the secondaries) above and/or below or else glabrous, with a rather distinct submarginal collecting vein. *Inflorescences* racemose-paniculate or subcapitate, laterally disposed on older denuded branches, red or reddish-purple, 0.5-8 cm long, pilosulous or glabrate. *Flowers* ☿, red, the distally articulated pedicels 0.5-4 mm long; calyx-segments 5, rotund-ovate, ca 1 mm long; petals 5, lanceolate to oblong- or ovate-lanceolate apically strongly uncinate (hooked inward), 2.5-3.5 mm long, erect or strongly ascending; stamens 10, subequal or unequal, slightly exceeded by the petals, the filaments flattened, tapering toward the apex; disc strongly crenate to subentire; styles (3-)4, 1 mm long or slightly less, ovate or ampulliform, glabrous, conspicuously constricted at the beginning of the capitate stigmatic portion. *Drupes* red or purple, 1.5-3.5 cm long, 1-2.5 cm broad, ovoid or oblong.

Southern Mexico, Central America and the West Indies to Brazil and Peru; cultivated in southern Florida.

BOCAS DEL TORO: region of Almirante, *Cooper* 355 (F, US). CANAL ZONE: Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper* 5772 (US); hospital grounds at Ancon, *Pittier* 2729 (US); Sosa Hill, Balboa, *Standley* 26485 (US); along the old Las Cruces Trail, betw Fort Clayton & Corozal, *Standley* 29122 (US); vic of Miraflores Locks, Madden Dam, Trans-Isthmian Hwy, *Stern et al.* 350 (MO, US); nr mouth of Cocoli River, *White* 98 (MO). CHIRIQUÍ: Progreso, *Cooper & Slater* 202 (US); Boquete Distr, *Davidson* 763 (F); Río San Cristobal, 2 mi W of David, *Tyson* 914 (MO). COCLÉ: Penonomé, *Williams* 380 (US). DARIEN: vic of El Real, Río Tuira, *Stern et al.* 795 (MO, US). PANAMA: along Chiva-Chiva Trail to Search Light Station beyond Chiva-Chiva, *Allen* 954 (MO); San José I, *Johnston* 573 (holotype of var. *munita* GH; isotype US), *Johnston* 1410 (MO); Bellavista, *Macbride* 2760 (F, US), *Standley* 25388 (US); Savana de Alhajuela, Chargres Valley, *Pittier* 3486 (US); banks of Mamoni River, below Chepo, *Pittier* 4692 (US); Tumba Muerto Rd, nr Panama, *Standley* 29779 (US); betw Matías Hernández & Juan Díaz, *Standley* 31940 (US); Taboga I, *Woodson et al.* 1511 (MO). PROVINCE UNKNOWN: "Western Panama," *Stork* 27 (US).

Spondias purpurea var. *munita* is not recognized as a distinct taxon in this treatment. In examining specimens assigned to this proposed segregate (including type specimens), no character was found which provides absolute separation from other specimens of *S. purpurea.* A feature considered by Johnston (loc. cit. 183) to be among those distinguishing var. *munita* is the rather striking serration of the

leaflets. However, the leaflets of many other specimens of *S. purpurea* show a greater or lesser amount of serration. The woody spines, reportedly characteristic of older branches of specimens of var. *munita,* were not present on the material available for study. Characters of the inflorescence, flower and fruit mentioned by Johnston do not serve to distinguish var. *munita.*

The plum-like fruits of the "red mombin" or "hog plum" are extensively eaten in tropical America, reportedly having a sweet-acid flavor.

2. **Spondias mombin** L., Sp. Pl. 371, 1753.—Fig. 5(A-D).

S. lutea L., Sp. Pl. ed. 2, 613, 1762.
S. lutea var. *maxima* Engler in Martius, Fl. Bras. **12**(2): 374, 1876.
S. lutea var. *glabra* Engler in Martius, loc. cit.
S. radlkoferi J. D. Sm., Bot. Gaz. **16:** 194, 1891.
S. nigrescens Pittier, Contr. U.S. Nat. Herb. **18:** 75, 1914.

Tree 6-27 m high with smooth or furrowed bark, the trunk straight. *Leaves* with 3-15 pairs of leaflets, the proximal leaflets alternate and the distal ± opposite, the rachis 7-35 cm long; lamina of leaflets oblong to somewhat ovate or obovate, apically acuminate or less frequently acute, basally acute to broadly obtuse, oblique and assymetric at the base, 5.5-14 cm long, 2-6.5 cm broad, membranous or subcoriaceous, glabrous or short-pilose on the nerves and along the margins; petiolules 2-7(-12) mm long (not including the petiolule of the terminal leaflet which is often longer). *Panicles* terminal, 15-40 cm long, minutely hirsutulous. *Flowers* ∞, ☿, 5-merous, the articulated pedicels 1.5-5 mm long; calyx-segments scale-like, ca 0.5 mm long, deltoid or deltoid-ovate; petals oblong-lanceolate or elliptic-lanceolate, apically uncinate, 2-3.5 mm long, spreading to reflexed, white or yellow; stamens 10, subequal, slightly shorter than the petals, the anthers ca 1 mm long, slightly curved, oblong-quadrate, relatively massive; disc strongly crenate (annular but virtually divided into 10 separate cushions); styles 5, ± linear, virtually unconstricted at the beginning of the stigmatic portion, glabrous, ca 1 mm long. *Drupes* ovoid to obovoid or oblong, 1.5-4 cm long, 1-2.5 cm broad, yellow.

Southern Mexico, Central America, the West Indies and tropical South America; introduced and naturalized in tropical Africa.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 504* (F), *Cooper & Slater 101* (US); Chiriquí Lagoon region, Chiriquicito, vic of Guarumo River, *Seibert 1555* (US). CANAL ZONE: Victoria Fill, nr Miraflores Locks, *Allen 1762* (F, MO, US); Barro Colorado I, *Carpenter 52* (F), *Dwyer 1458* (MO), *Kenoyer 420* (US), *Shattuck 82* (F, MO), *Starry 107* (F), *Wilson 113* (F), *Zetek 3414* (F), 3584 (F), *3611* (F, MO), 3645 (F, US), 3854 (MO); New Frijoles, *Christopherson 135* (US); U.S. Army Tropic Test Center, Miraflores Bridge, *Dwyer & Robyns 3* (MO); Albrook, U.S. Army Tropic Test Center Site, *Dwyer & Robyns 61* (MO); Chagres, *Fendler 141* (F, MO, US); around Bohio, Pittier 3423 (US); Summit, *Standley 26969* (US); along the Las Cruces Trail, betw Fort Clayton & Corozal, *Standley 29140* (US); Obispo, *Standley 31792* (US); Balboa, *Standley 32102* (US); vic of Miraflores Locks, edge of lake below spillway of Miraflores Dam, *Stern et al. 1* (MO); Miraflores Lake nr water plant, *Tyson 3553* (MO); Curundu Survival School Area, *Tyson & Dwyer 4457* (MO). CHIRIQUÍ: Progreso, *Cooper & Slater 207* (F, US). COCLÉ: betw Aguadulce & Antón, *Woodson et al. 1206* (F, MO). COLÓN: betw France Field, Canal Zone & Cativa1, *Standley 30401* (US). DARIEN: trail betw Pinogana & Yavisa, *Allen 272* (F, MO). PANAMA: Pedro Gonzalez I, *Allen 2598* (MO); San José I, *Erlanson 286* (US), *596* (US), *Johnston 746* (US); nr Chepo, *Kluge 34* (US); Trapiche I, *Miller 1877* (US), *1903* (US); Juan Díaz, *Standley 30464* (US); El Cermeño, *Zetek Z-4998* (F).

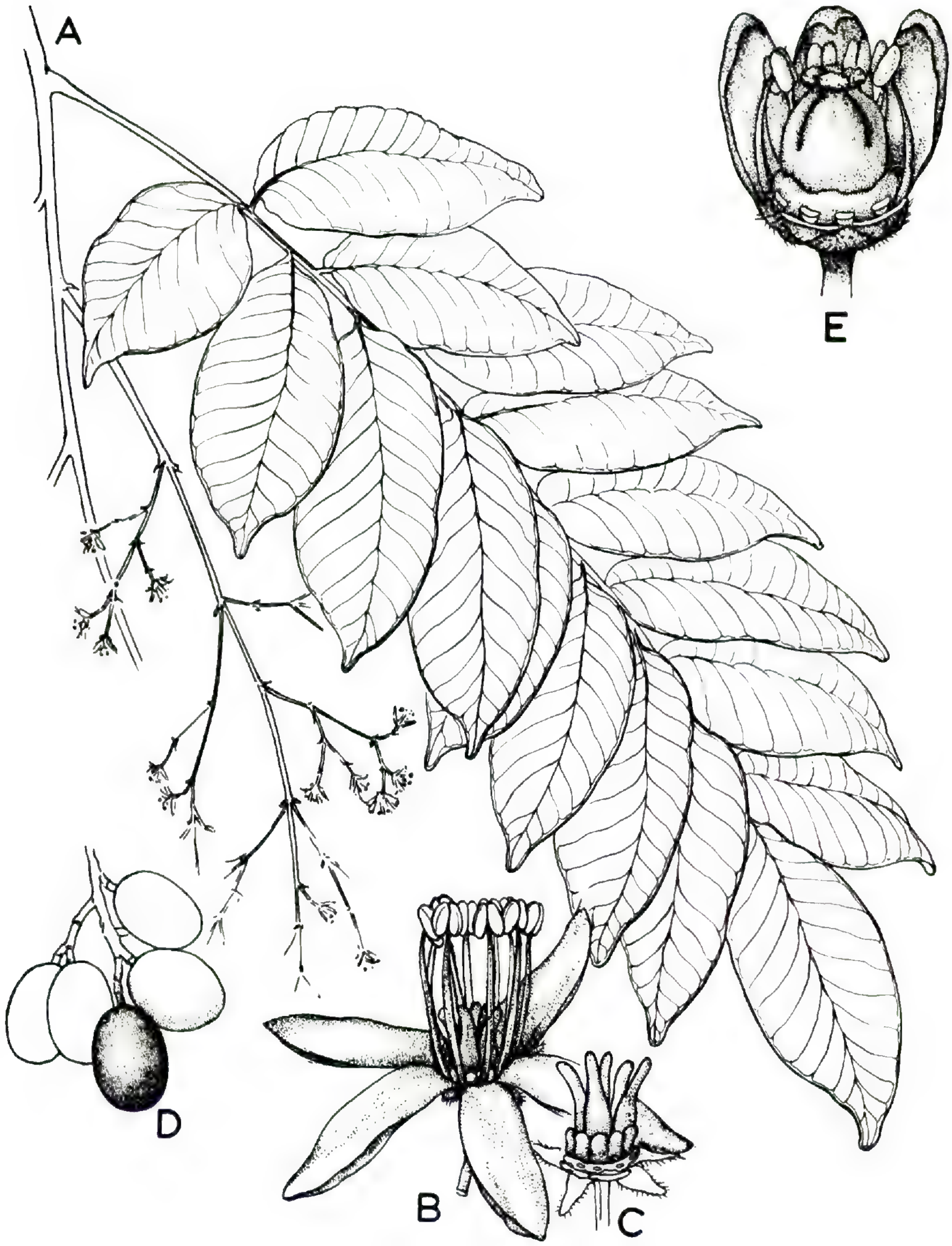

Fig. 5. *Spondias mombin* L.: A, habit (×⅔); B, flower (×6); C, id., petals and stamens removed (×9); D, drupes (×½). A-C after *Woodson et al. 1206* (MO); D after *Allen 2598* (MO). *Spondias purpurea* L.: E, flower, two petals and four stamens removed (×6). After *Johnston 1410* (MO).

Spondias mombin is regarded in this treatment as a polymorphic species. Examination of collections of *S. nigrescens* and *S. radlkoferi*, deposited at three major herbaria (F, MO, US), as well as the types of these species, indicated that they are forms of the highly variable *S. mombin*.

The fruit of this species is edible but is of inferior quality and is eaten less frequently than that of *S. purpurea*. The trees are sometimes used as living fence-posts.

6. MAURIA

Mauria Kunth, Ann. Sci. Nat., Bot., sér. 1, **2:** 338, 1824.

Shrubs to small trees. *Leaves* odd-pinnate to simple, the leaflets petiolulate. *Inflorescences* terminal or axillary panicles, often large. *Flowers* ☿ or less frequently polygamo-dioecious, short-pedicellate or sessile; calyx short-cupulate, distally with 4-5 shallow, broad teeth; petals 4-5, valvate or subvalvate; stamens 8-10, the filaments subulate, the anthers dorsifixed; disc intrastaminal; ovary 1-locular, the solitary ovule subapical, the style short, persistent, terminating in a 3-lobed stigma. *Fruit* drupaceous, compressed, the endocarp chartaceous; seed virtually filling the lumen of the drupe.

A genus of possibly 10-15 species much in need of monographic revision. Most of the species have been described on the basis of differences in leaf form and pubescence, characters which may be quite variable on an individual plant. The distribution of the genus is from Honduras to Peru and southern Brazil; one species is known to occur in Panama.

Mauria is closely related to the genus *Sorindeia* Dupetit-Thouars (Gen. Nov. Madag. 23, 1808) of tropical Africa. Marchand (Rév. Anacard. 167, 1869) treated *Mauria* as a section of *Sorindeia* and transferred the species of *Mauria* known at that time to *Sorindeia*. However, the majority of authors, both before and since Marchand, have recognized these two entities as separate genera. The latter view is adopted in this treatment as adequate discontinuity between them has been found. The virtually apical attachment of the ovule in the genus *Mauria* as well as the stamens always twice as many as the petals in the typically polygamous flowers would seem to merit generic distinction. That *Mauria* and *Sorindeia* are closely related genera, however, cannot be denied.

1. **Mauria heterophylla** H.B.K., Nov. Gen. Sp. Pl. **7:** 13, *t.* 606, 1824.—Fig. 6.

M. suaveolens Poeppig in Poeppig & Endl., Nov. Gen. Sp. Pl. **3:** 77, 1845.
M. puberula Tulasne, Ann. Sci. Nat., Bot., sér. 3, **6:** 363, 1846.
M. biringo Tulasne, loc. cit. 365.
Sorindeia glaberrima Engler in Martius, Fl. Bras. **12**(2): 392, 1876.
S. venulosa (Marchand) Engler in Martius, loc. cit.
Mauria heterophylla var. *puberula* (Tulasne) Engler in A. & C. DC., Monogr. Phan. **4:** 328, 1883.
M. biringo var. *granatensis* Engler in A. & C. DC., loc. cit. 329.
M. glauca J. D. Sm., Bot. Gaz. **23:** 5, 1897.

Shrub or tree to 20 m high. *Leaves* with 1-4 pairs of petiolulate leaflets, rarely simple on the same plant, the rachis 2-20 cm long; lamina of leaflets variable in

Fig. 6. *Mauria heterophylla* H.B.K.: A, habit (×⅔); B, flower (×7½); C, drupes (×⅔). A-B after *White* 33 (MO); C after *Allen* 3466 (MO).

shape (ovate, elliptic, oblong, lanceolate, obovate), apically acute or acuminate, less frequently obtuse or rounded at the apex, basally cuneate to rounded, usually asymmetric at the base, membranous or coriaceous, entire, 4-15 cm long, 1.5-7 cm broad, glabrous or else pubescent along the main nerves below (when pubescent beneath often barbate in the axils of the secondary veins), the secondaries often ± equally dichotomizing toward the margin, the reticulation usually prominent on both surfaces. *Panicles* terminal and axillary (from the upper nodes), 6-32 cm long, many-flowered. *Flowers* ☿, the pedicels 1-3 mm long; calyx cupular, 1-2 mm long, persistent, the 5 shallow lobes broadly deltoid; petals 5, white or yellow, erect or ascending, ovate-lanceolate or oblong-lanceolate, acute or subacuminate, 2-4 mm long; stamens 10, shorter than the petals; disc rather broad, 10-crenulate; ovary ovoid, 1-1.5 mm long, the style short, fleshy, glabrous, the stigmatic region minutely papillose, the ovule strongly compressed. *Drupes* obliquely ellipsoid or ovoid, 5-13 mm long.

Costa Rica, Panama and northern South America to Peru and Bolivia.

CHIRIQUÍ: llanos on slopes of Volcán de Chiriquí Viejo & along Río Chiriquí Viejo, *Allen 993* (US); Llano del Volcán, *Allen 3466* (F, MO, US); vic of El Boquete, *Maxon 5017* (F, US), *5149* (F, US); pastures around El Boquete, *Pittier 2897* (F, US); vic of Boquete, Llanos area just S of town, *Stern et al. 1944* (MO); Río Chiriquí Viejo valley, *White* 33 (MO), 55 (MO), *71* (F, MO), *234* (MO), *White & White 99* (MO). DARIEN: vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 936* (MO, US).

Examination of specimens of *Mauria biringo*, *M. glauca* and *M. suaveolens*, from Costa Rica, Panama and South America, deposited in MO, revealed no consistent morphological characters separating them from specimens of *M. heterophylla*. These species were based on leaf form and pubescence, characters which are often quite variable within a species and even on a single plant. The specific rank of these proposed segregates seems gravely in doubt and they have consequently been placed in the synonymy of *M. heterophylla*.

7. SCHINUS

Schinus L., Sp. Pl. 388, 1753; Gen. Pl. ed. 5, 184, 1754.

Trees or shrubs. *Leaves* simple or compound (the rachis often winged), the leaflets typically sessile or subsessile. *Inflorescences* paniculate, terminal or axillary, ∞-flowered. *Flowers* small, usually ♂ ♀ (at least functionally), the pedicels articulated; sepals 4-5, often ciliate marginally; petals 4-5, imbricate at anthesis, usually glabrous; stamens 8-10, those alternate with the petals almost as long as the petals in ♂ flowers, those opposite the petals ca ½ as long, all greatly reduced in ♀ flowers; disc cupular, not tumid, 8-10 crenulate; ovary unilocular, the solitary ovule suspended variously from near the middle to near the apex of the locule, the styles terminal, 3 or occasionally single, the stigmas 3. *Fruit* a small drupe as broad as long, the exocarp thin, lustrous, usually lavender or red, deciduous, the endocarp bony; seed compressed.

A genus of about 27 species native to South America; one species, possibly native, extends through Central America into Mexico. Several species are cultivated as ornamentals in tropic and warm-temperate regions of the New and Old World.

Useful reference:

Barkley F. A., *Schinus* L. Brittonia **5**: 160-198, 1944.

a. Leaves with 1-6 pairs of opposite leaflets; lamina of leaflets various but not narrowly lanceolate, with a length/width ratio of 1.3/1 to 3/1; style 1, the stigmas 3; ovule subapical .....1. *S. terebinthifolius*

aa. Leaves with 7-20 pairs of leaflets (often some of the leaflets alternate); lamina of leaflets rather narrowly lanceolate to linear-lanceolate, having a length/width ratio of 4/1 to 16/1; styles 3, free or confluent only at the base; ovule attached laterally to the ovary wall just above the middle of the locule .....2. *S. molle*

1. **Schinus terebinthifolius** Raddi, Mem. Mod. 18, *fig.* 399, 1820.—Fig. 7.

Shrub or tree to 7 m high, the branches glabrous or pubescent on young portions. *Leaves* imparipinnate, with 1-6 pairs of opposite leaflets, the rachis 3-14 cm long and often winged, the leaflets sessile or with petiolules to 1 mm long; lamina of leaflets obovate or elliptic to oblong or oblong-lanceolate, apically acute to rounded or rarely emarginate, occasionally mucronulate at the apex, basally cuneate, 1.5-7.5 cm long, 0.7-3.2 cm broad, having a length/width ratio of 1.3/1 to 3/1, entire or serrate, glabrous to conspicuously pilose, darker and often lustrous above, thickly membranous or subcoriaceous, the secondaries apparent, the reticulation obscure or subobscure. *Inflorescences* paniculate to subracemose, axillary, 1-11.5 cm long, conspicuously hirsute to glabrate. *Flowers* ♂ ♀ (a pistillode present in ♂ flowers, staminodes present in ♀ flowers), the pedicels 0.5-3 mm long; calyx-segments 5, deltoid, ca 0.75 mm long, often ciliate marginally; petals 5, ascending, oblong to ovate, apically rounded or subtruncate, white, 1.2-2.5 mm long, often curled outward at the tip; stamens 10, the anthers ovate and 0.5-0.8 mm long in ♂ flowers, the filaments compressed-subulate; disc 10-crenulate; ovary subglobose, ca 1 mm long, the ovule subapical, the style apparently single (the 3 styles confluent), 0.2-0.3 mm long, the stigmas 3, flattended, capitate. *Drupes* red, 4-6.5 mm long and broad.

A native of Brazil (and probably Paraguay), *S. terebinthifolius* is cultivated in Central America (possibly naturalized in the Canal Zone), Florida, California and in various parts of the Old World.

CANAL ZONE: region of Balboa, *Johansen 6* (US); Summit, *Mell 10* (MO, US); Balboa, *Standley 26897* (US).

The four Brazilian varieties of *S. terebinthifolius* recognized by Barkley are based on stem and leaf pubescence, leaflet number and angle of the leaflet apex. Brief examination of Brazilian specimens deposited in MO indicated that these taxa may represent nothing more than different points on a continuum of intergrading infraspecific variation in leaf and pubescence characters so often encountered in plant species. However, the authors do not assume the competence in the genus required to definitively evaluate the status of these varieties and for this reason they have not been placed in the synonymy of *S. terebinthifolius*.

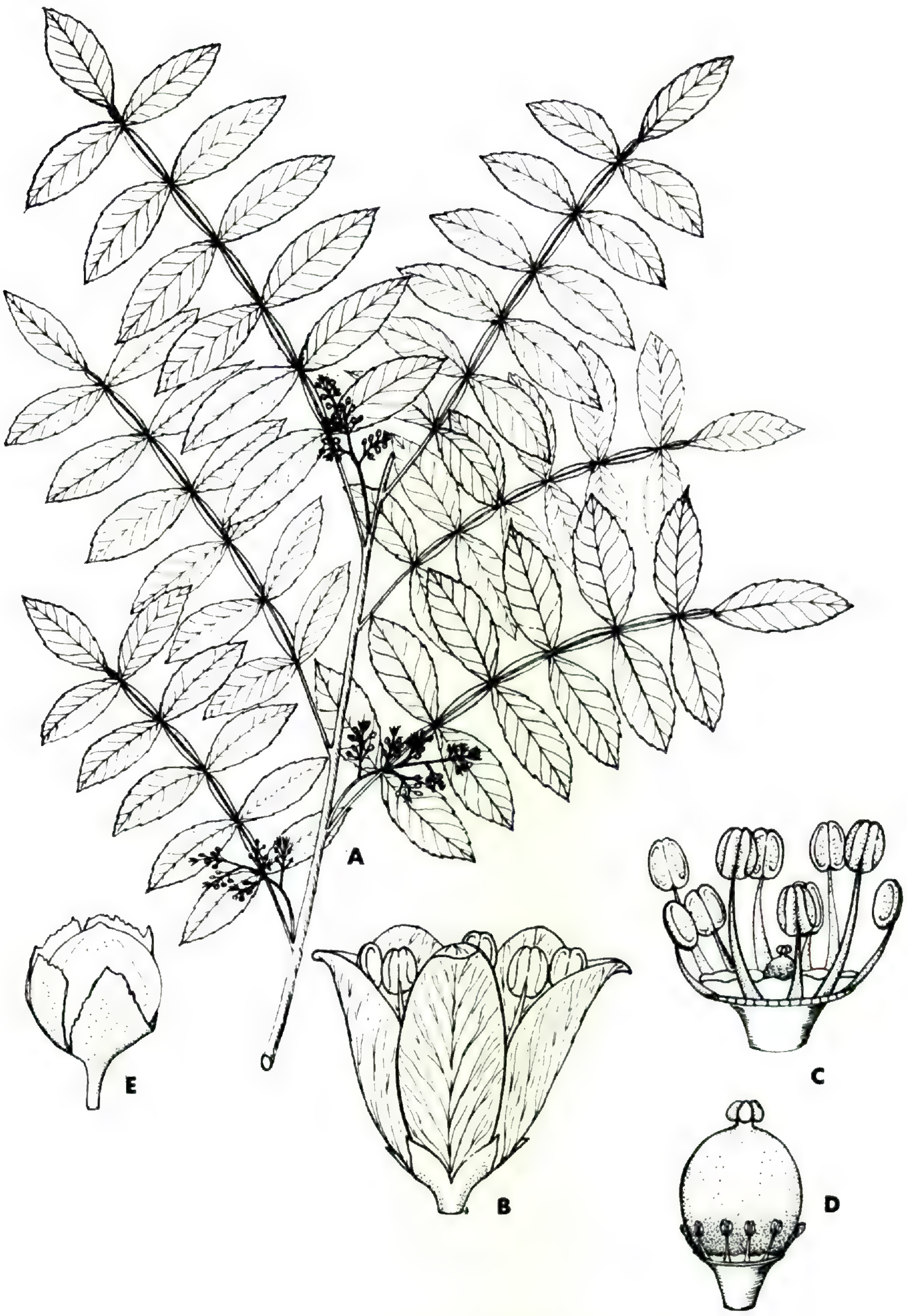

Fig. 7. *Schinus terebinthifolius* Raddi: A, habit (×½); B, functionally male flower (×12); C, id., calyx and corolla removed (×12); D, functionally female flower, calyx and corolla removed (×12); E, fruit with exocarp peeling (×3½). A after *Dusén 14324* (MO), Brazil; B-C after *Macedo* 3375 (MO), Brazil; D after *Bertoni* 3467 (MO), Argentina; E after *Lindman A1437* (MO), Brazil.

2. *Schinus molle* L., Sp. Pl. 388, 1753.

Schinus molle, the pepper tree, is noted for its handsome panicles loaded with yellowish-white flowers and the subsequent clusters of shiny, red or lavender fruits. It is cultivated as an ornamental in Mexico and Central America and has doubtless escaped from cultivation in many places. It is uncertain whether it is truly native to Mexico and Central America or was originally introduced from South America. The authors are not aware of the existence of a Panamanian collection of *S. molle,* but its occurrence in Panama seems probable.

8. ASTRONIUM

Astronium Jacquin, Enum. Syst. Pl. Carib. 10, 1760.

Myracrodruon Freire Allemao, Braz. Comm. Sci. Expl. Trab. Secc. Bot. 3, *t. 1 & 2,* 1862.

Trees, large or less frequently small. *Leaves* odd-pinnate, the leaflets usually opposite, entire or less frequently crenate or serrate, short-petiolulate. *Inflorescences* terminal or axillary, ∞-flowered. *Flowers* small, ☿ or ♂ ♀; calyx-segments 5, imbricate, persistent, accrescent and scarious in fruit; petals 5, imbricate in bud; disc 5-lobate, annular or the lobes ± sepaarte; stamens 5, inserted at the base or margin of the disc; ovary unilocular, the solitary ovule subapical, the styles 3, terminal, separate, short. *Fruit* drupaceous, narrowly oblong to ovoid or subglobose, ± terete, coriaceous, rostrate; seed oblong, the testa membranous.

About 12 species are known in tropical America; only one species is recognized in this treatment as occurring in Panama.

1. **Astronium graveolens** Jacquin, Enum. Syst. Pl. Carib. 33, 1760.—Fig. 8.

A. fraxinifolium Schott ex Sprengel in L., Syst. Veg. ed. 16, **4**(2): 404, 1827.

Tree to 35 m high. *Leaves* 2-7-jugate, the rachis 7-21 cm long (the petiole portion often elongate), the deciduous leaflets opposite (occasionally some alternate), with petiolules 1-6 mm long which are glabrous to pilosulous or villosulous; lamina of leaflets lance-oblong, less frequently ovate, acute or more often acuminate at the apex (the acumen obtuse to rounded or emarginate), basally obliquely acute to rounded or subtruncate, 4-14 cm long, 1.7-5 cm broad, membranous or subcoriaceous, entire or obscurely and irregularly crenate to serrate, glabrous to conspicuously pilosulous along the main veins below and often also above, occasionally generally pilosulous beneath, the secondaries often branching ± equally near the margin (dichotomous), the reticulation faint to prominent. *Panicles* terminal, 7-25 cm long. *Flowers* ♂ ♀ (staminodes are present in ♀ flowers but a pistillode is absent in ♂ flowers), the pedicels 1-15 mm long, articulated; sepals orbicular or infrequently ovate, 1-1.5 mm long in flower, becoming 9-14 mm long and elliptic to obovate or oblanceolate as the fruit matures, scarious in fruit; petals 1.5-3 mm long, oblong-ovate to elliptic, acute or rounded, ascending to spreading or reflexed; stamens 2-3 mm long, the filaments compressed and subulate, the anthers 1-1.5 mm long; disc flattened (not tumid); ovary ovoid-oblong, 1.5-2 mm long, the styles 0.5-1 mm long, persistent or deciduous, the stigmas small and disciform. *Fruit* narrowly oblong, 10-15 mm long at maturity, 2-4.5 mm broad, subterete, the mature seed filling the lumen.

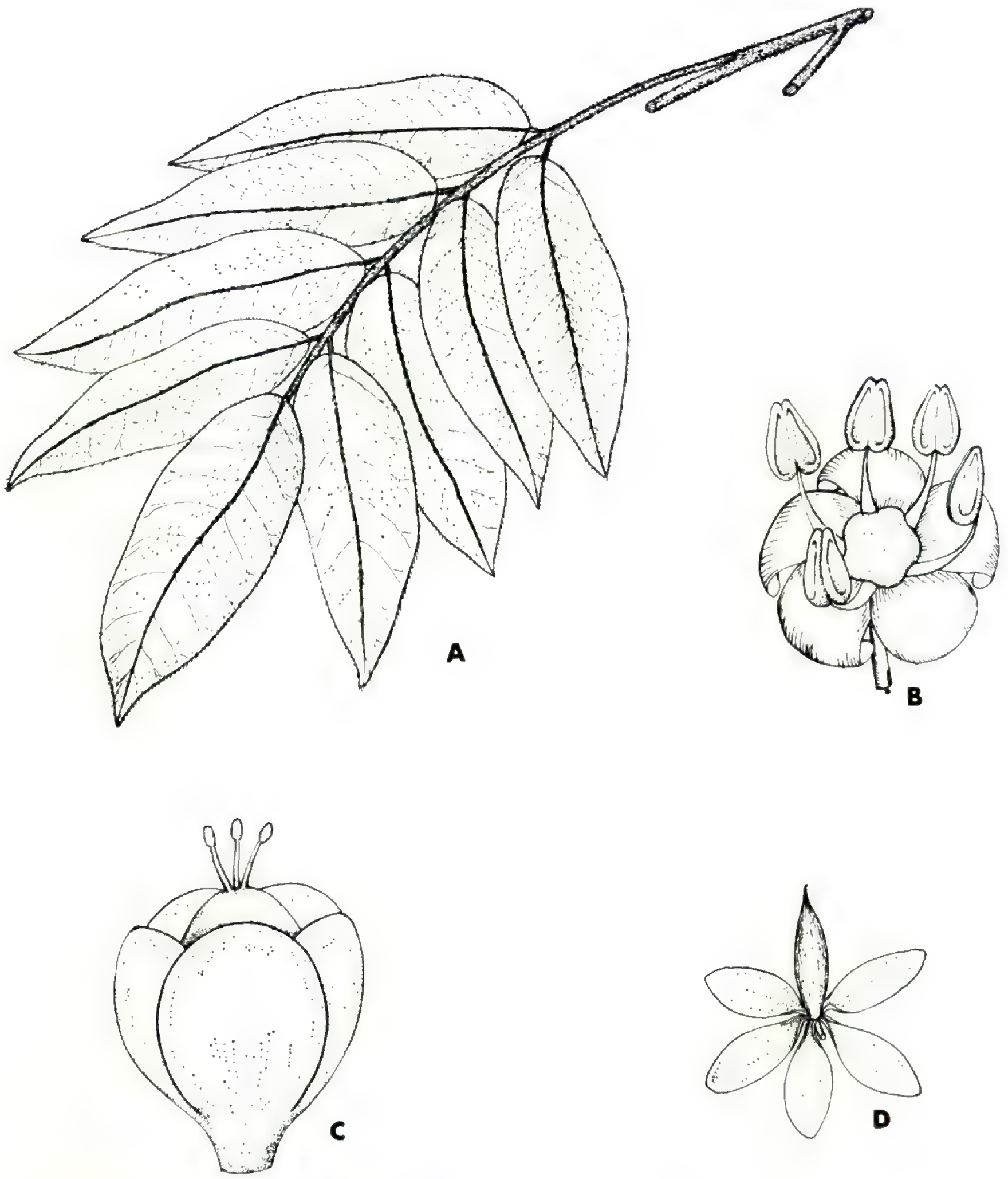

Fig. 8. *Astronium graveolens* Jacquin: A, compound leaf (×½); B, male flower (×7½); C, functionally female flower (×10); D, fruit and persistent sepals (×1). A, D after *Purpus 8761* (MO); Mexico; B after *Hassler 7151* (MO), Paraguay; C after *Hassler 91898a* (MO), Paraguay.

Southern Mexico, Central America and South America from Colombia to Brazil, Bolivia and Paraguay.

CANAL ZONE: Barro Colorado I, *Shattuck* 632 (F), 866 (F); Río Pedro Miguel, nr East Paraíso, *Standley 29951* (US). CHIRIQUÍ: Comarca del Barú, area W of Puerto Armuelles, *Stern & Chambers 129* (F, MO, US); Finca Lérida to Boquete, *Woodson et al. 1109* (F, MO). DARIEN: El Real de Sta. Maria, *Pittier 6997* (US). PANAMA: dry, wooded hills around Alhajuela, *Pittier 3730* (US); Río Tapia, *Standley 26183* (US); nr Matías Hernández, *Standley 28942* (US); Río Tocumen, *Standley 29377* (US); Juan Díaz, *Standley 30550* (US).

In both the Flora of Guatemala (Standley and Steyermark, Fieldiana: Bot. **24**(6): 180, 1949) and the Flora of Costa Rica (Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 624, 1937), *A. graveolens* and *A. fraxinifolium* are recognized as distinct species. In the Flora of Guatemala, however, a question is raised concerning the validity of separating specimens of *A. fraxinifolium* from Mexico and Petén from *A. graveolens*. The only character supposedly delimiting these species is the pubescence of the leaflets, being pilose in *A. fraxinifolium* and glabrous or essentially so in *A. graveolens*. After examination of Mexican, Central American and South American specimens of these taxa (deposited in F and MO), it appears that this distinction is arbitrary, as variation from completely glabrous to conspicuously pilose may be found in a very restricted geographic area. Specimens with an intermediate degree of pubescence are often encountered. Varietal status is the highest rank which could be accorded *A. fraxinifolium*. However, the authors have not recognized a variety *fraxinifolium* as they do not wish to apply formal names to extremes of a continuum of pubescence variation.

Wood of this species is of excellent grain and is used in furniture manufacture. It is also used for construction purposes but is apparently not insect resistant.

9. MOSQUITOXYLUM

Mosquitoxylum Krug & Urban, Notizbl. K. Bot. Gart. Mus. Berlin **1:** 78, 1895.

Trees. *Leaves* imparipinnate, ± persistent, the leaflets opposite or subopposite; lamina of leaflets subcoriaceous, glabrate to soft-pubescent above and below, entire. *Panicles* arising from the upper leaf-axils, the branches spicate. *Flowers* small, mostly ☿ ; sepals 5, free, persistent, imbricate; petals 5, imbricate in bud; stamens 5, inserted at the margin of the disc; ovary 1-locular, the ovule affixed laterally near the base of the locule, the style terminal, short, 3-branched near the apex, the stigmas 3. *Drupes* obliquely ovoid, compressed; seed latero-basal, small (occupying only a small portion of the fruit lumen).

A monotypic genus occurring in Mexico, Central America and the West Indies.

Mosquitoxylum jamaicense Krug & Urban, Notizbl. K. Bot. Gart. Mus. Berlin **1:** 79, 1895.—Fig. 9.

M. jamaicense var. *panamense* Barkley & Reed, Amer. Midl. Nat. **24:** 677, 1940.

Tree to 30 m high; branches with scurfy, gray or grayish-brown bark, the elliptical lenticels often prominent. *Leaves* clustered toward the branch-tips, with 5-14

Fig. 9. *Mosquitoxylum jamaicense* Krug & Urban: A, habit (×½); B, flower (×7½); C, id., sepals and petals removed (×9½). After *Woodson et al. 1245* (MO).

pairs of leaflets, the rachis 10-30 cm long, the leaflets short-petiolulate; lamina of leaflets oblong to oblanceolate or obovate, apically rounded or emarginate or obtuse to acute or short-acuminate, basally cuneate and unequal, 2.5-8.5 cm long, 1.2-3 cm broad, marginally subrevolute, pilose above and below or glabrate. *Panicles* 7-27 cm long, the branches hirtellous. *Flowers* sessile, not clustered, each subtended by 3 persistent deltoid bracts ca 1 mm long; sepals ovate or rotund-ovate, ca 1 mm long, marginally minutely ciliate; petals ascending, ovate or elliptic, sparsely pubescent on the inner surface, 1.5-2 mm long; stamens ca 1 mm long; disc 5-lobate (each lobe secondarily lobed, the disc thus 10-crenulate), cupular; style persistent, the stigma ± capitate. *Drupes* scarlet, lustrous, glabrous, 6-9 mm long, the mesocarp thin; seed somewhat compressed.

CANAL ZONE: Barro Colorado I, *Aviles 23b* (F), *955* (F), *Bangham 426* (F). COCLÉ: Loma del Tigre, region N of El Valle de Antón, *Allen 3805* (MO); betw Las Margaritas & El Valle, *Woodson et al. 1254* (F, MO). COLÓN: Loma de la Gloria, nr Fató (Nombre de Dios), Pittier *4143* (holotype var. *panamense* B; isotypes GH, US). DARIEN: Puerta St. Dorothea, *Dwyer 2200* (MO), *2266* (MO, US).

The variety *panamense* proposed by Barkley and Reed is not recognized. With respect to the supposedly distinguishing characteristics of the varieties (leaflet number and pubescence), an isotype specimen (GH) of var. *panamense* has been found to conform more closely to var. *jamaicense* than to var. *panamense*. Examination of Central American specimens deposited in MO indicates that variation in leaflet number and pubescence is at random and completely intergrading within the species population. Two entities could not be said to exist in such a situation.

Mosquitoxylum jamaicense, known as mosquito wood, is valued for building purposes.

10. TOXICODENDRON

Toxicodendron P. Miller, Gard. Dict. Abr. ed. 4, 1754.

Rhus L., Sp. Pl. 265, 1753, pro parte.

Trees, shrubs or woody lianas with poisonous secretions. *Leaves* imparipinnate, deciduous, the leaflets membranous. *Inflorescences* paniculate, axillary, erect to nodding or pendant, the bracts lanceolate and deciduous. *Flowers* small, polygamodioecious; sepals 5, persistent; petals 5, ascending to spreading or reflexed, imbricate at anthesis; stamens 5, inserted below the disc; ovary 1-locular, sessile on the disc, the ovule basal, the style terminal, simple or apparently so, the stigmas 3. *Drupes* white, ca as long as broad, glabrous or sparingly pubescent with simple (eglandular) trichomes, slightly compressed, the exocarp deciduous, the mesocarp richly ceriferous; seed compressed.

Many authors (e.g., Engler in A. & C. DC., Monogr. Phan. **4:** 393, 1883) have treated *Toxicodendron* as part of the genus *Rhus* L. However, Barkley (Ann. Missouri Bot. Gard. **24:** 419, 1937) presents considerable evidence that *Toxicodendron* is a distinct genus. Five species are recognized by Barkley in the Western Hemisphere, one occurring in Panama. There are several Asian species. All members of the genus possess an irritant poison in the stem and leaves (and often in

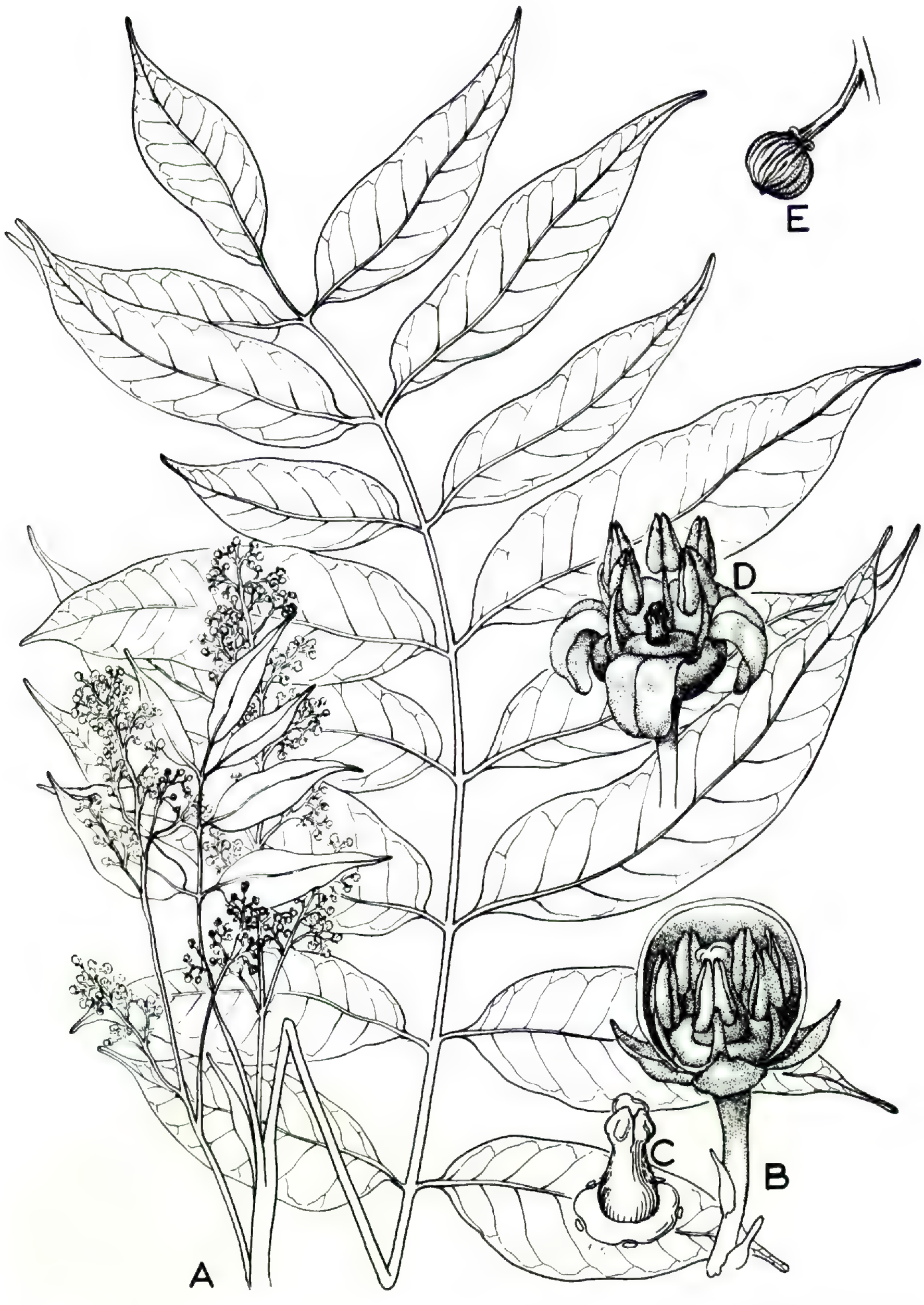

Fig. 10. *Toxicodendron striatum* (Ruiz & Pavon) Kuntze: A, habit (×⅔); B, bud of ♀ flower (×17); C, pistil and disc (×14); D, functionally ♂ flower (×8); E, drupe after epicarp has fallen away (×1⅓). A, B & E after *Woodson & Schery 483* (MO); C after *Purpus 7378* (MO), Mexico; D after *Purpus 2019* (MO), Mexico.

the flowers) causing dermatoses in many individuals. Poison oak, *T. radicans* (L.) Kuntze, is a member of this genus. The sap of *Toxicodendron* species has the property of becoming black on exposure to air and drying into a durable varnish.

1. **Toxicodendron striatum** (Ruiz & Pavon) O. Ktze, Rev. Gen. Pl. **1:** 153, 1891.—Fig. 10.

Rhus striatum Ruiz & Pavon, Fl. Peruv. Chil. **3:** 29, *pl.* 252, 1802.
R. juglandifolia Willd. ex Roemer & Schultes in L., Syst. Veg. ed. 15, **6:** 649, 1820.
R. samo Tulasne, Ann. Sci. Nat., Bot., sér. 3, **6:** 367, 1846.
R. juglandifolia var. *samo* (Tulasne) Engler in A. & C. DC., Monogr. Phan. **4:** 401, 1883.

Tree or large shrub. *Leaves* 4-8 jugate, the rachis 10-30 cm long, the leaflets mostly opposite, with petiolules 2-6 mm long; lamina of leaflets oblong-lanceolate to oblong or occasionally ovate-lanceolate, apically acuminate, basally unequal and broadly cuneate to rounded, 5-11 cm long, 2.5-5 cm broad, entire and often subrevolute, glabrous or puberulent beneath on the main veins. *Panicles* large, erect to ± pendant, ∞-flowered, the branches hirtellous. *Flowers* apparently ♂ (pistillode present) or ☿ (stamens somewhat reduced), the pedicels 1-4.5 mm long; sepals suborbicular to ovate-oblong, apically rounded or subtruncate, ca 1 mm long; petals ovate or oblong-ovate, 2-3 mm long; anthers 1.5-2 mm long in ♂ flowers, smaller in ☿ flowers, lanceolate or ovate-lanceolate, basally ± cordate, the filaments compressed and subulate, 1.5-2 mm long in ♂ flowers; disc flattened, not tumid, obscurely 5-10 crenulate; ovary ovoid, ca 0.8 mm long, the style less than 0.5 mm long, persistent, the stigmas minutely papillose, capitate, flattened, subobscure. *Drupes* 5-9 mm long, white, the surface of the mesocarp with conspicuous dark, longitudinal streaks; seed filling the lumen of the drupe, 5-8 mm broad.

Vera Cruz, Mexico to Brazil and Peru.

CHIRIQUÍ: forests around El Boquete, *Pittier 3029* (US); vic of Callejón Seco, Volcán de Chiriquí, *Woodson & Schery 483* (MO, US).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 102. AQUIFOLIACEAE[1]

BY GABRIEL EDWIN
Field Museum of Natural History, Chicago, Illinois

Trees or shrubs, dioecious, glabrous or pubescent with simple, short hairs. *Leaves* simple, alternate, petiolate, rarely (2 species of *Ilex* in Borneo) opposite and sessile, the venation reticulate, the small free stipules soon fugacious. *Flowers* solitary to variously elaborately grouped into cymes (incl. dichasia), racemes, panicles or umbels, these regular or irregular (basically a trichotomous cyme or once-branched dichasium), borne axillarily or laterally, on new or old wood; unisexual by abortion, a rudiment of the aborted part present; 4- to 20- (or more) merous, usually isomerous (except for the aborted portion); sepals united into a short calyx tube or free; petals united into a short corolla tube or free; anthers introresly dehiscent, the filaments adnate to the base of the corolla tube (when present) and opposite the calyx lobes or free; ovary when fertile with locules as many as the petals, disorganized when sterile (pistillodium), the sterile androecium represented by staminodia; style usually lacking or very short; stigmas various, punctiform to disc-like; ovules anatropous; placentation axile; entire flower rarely exceeding 25 mm in diam, frequently not exceeding 10 mm. *Fruit* a bacco-drupa, usually round or almost so, ca 3-20 mm in diam with 1 seed in each locule (very rarely 2 in each); embryo red, small in copious fleshy endosperm[2].

A family of three genera generally distributed throughout the temperate and tropic zones, deserts excepted. *Phelline* with about 20 species is found in Tasmania, New Zealand and Australia; *Nemopanthus,* one species in the northeastern United States and southeastern Canada; *Ilex* with 550-650 species world-wide and the only genus of the family in Panama where four species have been reported (cf. Loesener, Monographia Aquifoliacearum, Abh. K. L.-C. Deutsch. Akad. Naturf. **78:** 1-567, *15 t.*, 1901 & **89:** 5-314, *2 maps*, 1908).

1. ILEX

Ilex L., Sp. Pl. 125, 1753; Gen. Pl. ed. 5, 158, 1754.

Trees or shrubs, the branchlets all elongated or elongated and abbreviated. *Leaves* with the blades linear to suborbicular, usually persistent (Panama), stipu-

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

[2] A plate explaining the application of most of the descriptive terms may be found in Mem. N. Y. Bot. Gard. **12:** 126, 1965.

late, from very short- to moderately long-petiolate, the margins entire or variously toothed, cut or spinose, glabrous or puberulent, rarely pilose, especially beneath, membranaceous to thickly coriaceous, usually shining and dark green above, paler and duller beneath. *Flowers* on current growth or on old wood, solitary or fasciculate, usually axillary to a leaf or forking of branchlets, or laterally single, or singly clustered laterally or axillary at the base of current growth, the clusters one- to many-flowered, forming cyme-like, dichasiate, racemose, corymbose, umbellate, paniculate, or irregularly complex, usually determinate inflorescences, mostly 4-merous, varying (New World) from 4- to 8-(9-)merous (aborted ♀ organs excepted), isomerous; calyx usually imbricate, patelliform to cupuliform, in fruit frequently becoming explanate, the lobes shorter, equal to or longer than the tube, usually ovate or deltoid, occasionally irregular, entire or laciniate, ciliolate or eciliolate, acute or obtuse; corolla imbricate, rotate, the petals united at the base (rarely, but not in ours, almost free), usually white, rarely greenish-white, yellowish-white, or pinkish-white; filaments usually shorter than but varying to little longer than the petals, thickened at the base; fertile stamens with anthers longer to shorter than the filaments; staminodia with aborted anthers mostly shorter than the filaments, occasionally subobsolete; fertile ovary mostly conic, ovoid or ellipsoid, the style usually lacking, the stigmatic lobes sessile, equal in number to the locules of the ovary, usually united into a punctate to hemispherical stigma, when style present, the stigma subsessile; locules 1-ovulate, the ovules with 1 integument; pistillodium very variable, usually conic to pulvinate, the style usually lacking, the stigmatic lobes free, partly conflent or united, much smaller than the fertile ovary. *Fruit* ellipsoid to globose, mostly red, sometimes black or dark violet, rarely yellow or white, the calyx and stigma persistent; exocarp usually thin; mesocarp mostly thick, sometimes almost lacking; endocarp mostly hard, coriaecous to stony, surrounding and united with a seed to form a pyrene; pyrenes mostly trigonous, sometimes lanceolate in cross-section, equal to the number of locules of the ovary, in ours 4-8(-10), dorsally smooth or variously striate, sulcate, ridged or canaliculate, laterally smooth to marked (as dorsally), ventrally reduced to a stria.

The center of distribution is in the Western Hemisphere in the area between the Río La Plata and eastern Andes from northern Argentina to southeastern Colombia.

a. Blades mostly widest above the middle, variously obovate, or very broadly obovate or suborbicular, when suborbicular, the teeth shallow, few or lacking, crenulate; ♂ flowers usually fasciculate; calyx lobes acuminate or acute.
  b. Blades, obovate, usually 2× or more longer than wide, with margins essentially entire (occasionally few-toothed); ♂ flowers usually pedunculate; calyx-lobes acute ..... 1. *I. guianensis*
  bb. Blades suborbicular or very broadly obovate, less than 2× as long as wide, the margins appressed-crenulate, at least on the upper ⅓ of the blade; ♂ flowers pedicellate; calyx-lobes acuminate ..... 2. *I. chiriquensis*
aa. Blades widest at or below the middle, very broadly cuneate-ovate to suborbicular, or elliptic to broadly elliptic, when suborbicular, the teeth deep and many, dentate; ♂ flowers (where known) mostly solitary; calyx lobes obtuse.
  c. Blade margins entire ..... 3. *I. valerii*
  cc. Blade margins grossly dentate ..... 4. *I. discolor* var. *lamprophylla*

1. **Ilex guianensis** (Aublet) O. Ktze., Rev. Gen. Pl. **1:** 113, 1891; Johnston, Sargentia **8:** 189, 1949.

Macoucoua guianensis Aublet, Hist. Pl. Gui. Fr. 88, *t.* 34, 1775.
Ilex panamensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 221, 1952.

Tree, evergreen, up to 15-20 (-25) m tall, the branches drying ashy grey to blackish, rarely light grey, glabrous, the branchlets glabrous or puberulent, the current wood puberulent with soft, short, white hairs, rarely glabrous, the puberulence sometimes scattered, striatulate when dry. *Leaves* with the blades coriaceous, sometimes thickly chartaceous, glabrous, or with a very few hairs on the costa beneath, infrequently very asymmetrical, rarely both symmetrical and asymmetrical leaves on a single branch, (3.1-)4-12.5(-15.6) cm long, (1.1-)2-5 cm broad, obovate, elliptic-obovate, narrowly obovate, sometimes oblong, elliptical, subspathulate-obovate or sublanceolate, the margins entire, sometimes a little thickened and revolute, rarely few-serrate or dentate, the apex acute or (short-) acuminate, sometimes rounded obtuse or acuminately obtuse, rarely rounded-retuse or short-apiculate (last fide Loesener), the base acute or cuneately acute, less often cuneate or long- or subspathulately acute, usually thinly decurrent over the entire length of the petiole, epunctate, puncticulate or punctate, the costa impressed above, elevated beneath, the veins and veinlets generally subobsolete to little conspicuous above and beneath; petiole mostly 6-14 mm long, usually a little thickened, often blackening in drying, usually sparsely puberulent with very short hairs, occasionally subglabrous, rarely glabrous. *Flowers* and inflorescences borne on new and old wood, axillary, lateral, fasciculate, rarely solitary, 4- or rarely 5- merous; ♂ flowers pedunculate, rarely merely pedicellate; ♀ flowers pedicellate, rarely pedunculate; ♂ flowers borne on glabrous or puberulent pedicels, forming a fascicle of cymes or cyme-like inflorescences, rarely the peduncle either regularly or irregularly 2× branched forming a paniculate inflorescence, very rarely 3× branched, the peduncles (1.5-) 3-11(-14) mm long, usually 4-7 mm, the pedicels ½ or frequently less than ½, usually ⅓-¼ the length of the peduncle, rarely especially in bud a little more than ½ the length of the peduncle; calyx glabrous, the lobes ca equaling to a little longer than the tube, broadly deltoid-triangular, usually acute, the margins eciliolate; petals 2.5-3 mm long, ca 1.7-2 mm broad, ovate, usually obtuse; stamens mostly a little longer than the petals, occasionally equal to or little shorter than the petals, the anthers mostly ⅓-½ the lenght of the filament, rarely almost equaling, oblong or narrowly ovate, narrowed near the apex, rarely oblong-sagittate; pistillodium usually constricted near the apex, pulvinate, sometimes broadly ovoid or conical, a rudimentary punctate stigma frequently present; ♀ flowers with the pedicels puberulent, up to 7.5 mm long, usually ca 2-4 mm long; calyx-tube occasionally sparsely puberulent; margins of the petals rarely remotely laciniate, otherwise perianth as in the ♂ flower; staminodes a little shorter than the petals and a little longer than the ovary, the sterile anthers much shorter than the filaments, broadly ovate-sagittate; ovary ca 1.75 cm long, broadly ovoid to subglobose or rarely globose, the stigma sessile, discoid. *Fruit* red or dark red in life, drying brown or occasionally blackish-brown, subglobose to globose, usually 4.5-

5.5(-6.5) mm long, 4.5-5(-7) mm in diam, smooth, the stigma punctate-discoid to subcoronate; mesocarp medium to subcopious; pyrenes 4, rarely 5, trigonous to broadly trigonous, dorsally usually smooth, occasionally unisulcate or shallowly unicanaliculate, a striatula sometimes in the sulcation, laterally smooth or with a gibbosity, ventrally blunt, occasionally 1 or 2 pyrenes aborted and sterile, when fertile 4.5-5 mm long, 1.5-2 mm broad, laterally vascular tissue (striae) often loosely adnate to the pyrene; endocarp medium hard, ligneous.

BOCAS DEL TORO: Bocas I, Almirante, *Cooper 469* (NY, type of *I. panamensis*). CHIRIQUÍ. Bajo Chorro, Boquete, *Davidson 254* (MO). COCLÉ: vic of El Valle, *Allen 752* (MICH, MO), *2505* (US), *3570* (MO, US). PANAMA: San José I, *Erlanson 77* (MICH, NY, US), *260* (US), *348* (NY, US), *411* (US), *513* (MICH, US), *Johnston 224* (US), *341* (MO, US,) *426* (US).

2. **Ilex chiriquensis** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 88, 1940.

Shrub, evergreen, wholly glabrous. *Leaves* with the blades very broadly cuneate-obovate to subcircular, the base cuneate or acute, decurrent over the petiole, thickly at the apex diminishing to thin wing-like decurrency over the lower ¾-⅘, (3.3-)3.8-5.3(-6) cm long, (2.2-)2.8-4.8 cm broad, shining or brown-green above, paler and duller beneath, punctate, the punctations red, turning black, thickly coriaceous, the margins thickened, revolute, distantly appressed-crenulate, the crenulations callosed or spine-tipped, mostly on the upper ⅓ of the margin and less distant near the rounded apex of the blade, the costa plane or little impressed above, little elevated beneath, the veins and veinlets ± obsolete above, inconspicuous beneath; petiole thickened, turning black when dry, mostly 9-12 mm long. ♂ *flowers* (from buds) mostly borne at the base of new wood, usually fasciculate, sometimes aggregated-subfasciculate, axillary to leaves or nodes, occasionally laterally fasciculate directly on old wood (very rarely apparently from a mixed bud), pedicellate, 4-(5-)merous; pedicels up to 3 mm long; calyx-lobes longer than the tube, broadly ovate, obtuse; immature petals only ca 1.5 mm long, ovate; immature stamens ca 1 mm long, anthers oblong to ovate, dark brown to black, much exceeding the thickened black filaments; pistillodium pulvinate to ovoid, a conic style developed or not. ♀ *flowers unknown. Fruit unknown.*

CHIRIQUÍ: rain forest, Bajo Chorro, Boquete, alt 6000 ft (♂), *Davidson 243* (holotype MO, isotype US).

The material is scanty and immature. The above description is partly interpretive, especially as to where the flowers are borne and whether or not mixed buds develop. The distinctive foliage is similar to *I. hondurensis* Standley which differs in blades being epunctate and not subcircular (only rarely so). The foliage of *I. chiriquensis* is also similar to *I. subrotundifolia* Steyerm. of the Guayana Highlands, which differs in having very much shorter petioles and entire leaf-margins.

3. **Ilex valerii** Standley, Jour. Wash. Acad. Sci. **16:** 483, 1926.

Tree, evergreen, up to 25 m tall; branches glabrous. *Leaves* with the blades thinly to thickly coriaceous, glabrous (3-)4.3-10 cm long, (1.7-)2.6-4.5 cm broad,

mostly ovate or subovate, less often elliptical to broadly elliptical or elliptically ovate, the margins entire, a little revolute and thickened, the apex acute or acuminate, the base acute to more often obtuse, sometimes asymmetrical, decurrent over the petiole, drying shining or subshining, dark green, brown-green or black above, duller and paler beneath, epunctate, the costa little impressed or plane above, little elevated beneath, the veins and veinlets subobsolete to obsolete above, visible beneath; petioles glabrous, rarely scattered-puberulent, thickened, (6-)8-21(-23) mm long. *Flowers* all or mostly on this year's wood; ♂ flower pedunculate, forming small cyme-like or rarely subumbelliform inflorescences, mostly on new, occasionally on last year's wood, axillary, solitary, 4-5-merous; peduncles 7-27 mm long, glabrous or very sparsely, scattered puberulent, pedicels either ca ½ or little less or 1/7-1/9 the length of the peduncle; calyx-tube 0.4-0.7 mm long, glabrous, much shorter than the broadly ovate, abruptly acuminate, usually glabrous, sometimes sparsely ciliolate lobes, the entire calyx ca 1.7-2.2 mm broad; petals broadly ovate, obtuse, ca 3-3.5 mm long, 1.7-1.9 mm broad; stamens ca 1.8 mm long, the anthers ca equaling the filaments in length, very broadly ovate or broadly ovate-cordate, or broadly oblong or oblong-subsagittate, the filament thickened, extending upward between the anthers; pistillodium conic or ovoid-conic, ca 1.4-1.8 mm long, the stigmatic lobes wholly united; ♀ flowers (from immature fruit, very few seen) borne on new wood, axillary, solitary, pedicellate, 4-5 merous; pedicels glabrous or very sparsely, very short-puberulent, 7-11 mm long; calyx as in the ♂ flowers. *Fruit* (immature) drying black, smooth to rugulose, ellipsoid-subglobose, ca 5 mm long, 4 mm broad, the stigma punctate-subcoronate; endocarp copious; immature pyrenes 4, trigonous, dorsally smooth or shallowly canaliculate, ca 3 mm long, 1.15 mm broad, laterally apparently smooth; endocrap soft.

a. Petioles mostly 15-23 mm long; ♂ peduncles 17-27 mm long; ♂ pedicels mostly 1/7-1/9 the length of the peduncles; a few flowers on last years wood ..... 3a. *I. valerii* var. *valerii*

b. Petioles mostly (6-)8-13 mm long; ♂ peduncles 7-11 mm long; ♂ pedicels ½ to a little less as long as the peduncles; all flowers on current wood ..... 3b. *I. valerii* var. *ramonensis*

3a. *I. valerii* Standley var. *valerii*.

Costa Rica, Panama.

CHIRIQUÍ: s. loc., *Davidson* 822 (US).

3b. *I. valerii* Standley var. *ramonensis* (Standley) Edwin, Ann. Missouri Bot. Gard. **54:** 184, 1967.

I. ramonensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 630, 1937.

Differing from the typical as noted in the key and with the perianth mostly a little smaller and also the mature leaf-blades a little thicker.

The Panamanian collection is the only collection other than the type (Costa Rica).

CHIRIQUÍ: El Boquete, Holcomb's Trail, *Killip* 3562*a* (US).

4. **Ilex discolor** Hemsley var. **lamprophylla** (Standley) Edwin, Ann. Missouri Bot. Gard. **53:** 376, 1966.

I. lamprophylla Standley, Jour. Wash. Acad. Sci. **15:** 476, 1925.
I. carpenterae Standley, loc. cit. 477.
I. davidsoniae Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 88, 1940.

Tree, shrub or rarely liana, evergreen, up to 9 m, the branches and older branchlets drying dark grey, grey-brown, light or dark brown, the young wood glabrous to densely puberulent, with very short, white hairs, the older wood glabrous, glabrate or rarely very short-puberulent. *Leaves* with the blades usually 2 or more times longer than wide, very variable, 4.5-11.5(-13) cm long, 0.8-5.7(-6.6) cm wide, ovate or obovate or elliptical, sometimes spathulate-obovate or lanceolate-obovate, sometimes one branch bearing leaf-blades with two different shapes, glabrous or puberulent on the costa below, the margins crenate or crenulate, less often dentate, sometimes serrate-serrulate, especially below the middle, or subentire, the teeth with or without a short, thickened spine, the apex mostly acuminate, the base mostly acute to infrequently narrowly cuneate, usually narrowly decurrent the length of the petiole, drying shining bright green to black above, paler and duller beneath, punctate, puncticulate or epunctate, the veins conspicuous to subobsolete; petioles glabrous to densely puberulent, not thickened, 3.5-10 mm long. *Inflorescences* axillary, fasciculate, the ♂ on new wood, the ♀ mostly on new, sometimes on old wood; ♂ inflorescences plurifasciculate. ♂ *flowers* white to green, 4-(5-)merous, mostly pedunculate, sometimes pedicellate, usually glabrous, sometimes the pedicel, peduncle and calyx puberulent, the calyx-lobes sometimes also ciliolate; peduncles 1× branched into 2 or 5 pedicels forming cyme-like inflorescences or 2× branched either regularly or irregularly, forming compound cymes or racemose or paniculate inflorescences; peduncles from 0.5-5 mm long; pedicels 1-4.5 mm long; calyx 1.3-3.2 mm long, the tube short, the lobes ovate, broadly rounded to acute; petals 2.2-2.5 mm long, narrowly to broadly ovate, usually obtuse; stamens little shorter than the petals, the anthers and thickened filaments subequal, the anthers usually oblong or subulate or conic; pistillodium ovoid, ca 1.3 mm long, narrowed below the stigmatic-lobes, the latter usually at least partly united to form a subhemispherical stigma. ♀ *flowers* white to green, 4-(5-)merous, pedicellate, few-(2-7-)fasciculate, rarely solitary; pedicels glabrous to puberulent, 0.5-3 mm long; perianth as in the ♂ flowers; staminodes shorter than the petals, longer or shorter than the ovary, the sterile anthers very short, ca 0.5 mm long, cordate, much shorter than the filament; ovary ovoid, ca 2 mm long; stigma large, capitate-subcoronate, the 4 lobes not completely confluent. *Fruit* red (reported also green, but immature), smooth or striate, ellipsoid, 3.5-6 mm long, 2.5-5 mm in diam, the stigma often on a short style, coronate, or when sessile, punctate to subcapitate; calyx explanate; mesocarp scanty to submedium; pyrenes 4(-5), trigonous, 3-5-striate-sulcate dorsally, 1-3-striate-striatulate laterally, a dull stria ventrally, 3.5-4 mm long, 2 mm broad; endocarp soft.

All material from Panama (and Costa Rica) has obviously toothed blades;

however, blades vary to subentire in Honduras and this condition may be found in Panama.

CHIRIQUÍ: s. loc., *Davidson 166* (holotype *I. davidsoniae* F, isotype MO).

Not yet reported but likely to be encountered in Panama are: *Ilex paraguariensis* St.-Hil., with flowers in dense compound inflorescences on both new and old wood; *I. macfadyenii* (Walp.) Rehder, with lanceolate pyrenes in a dense central cluster in the fruit; and another variety of *I. discolor* from wet forests of Costa Rica with obtusely rounded leaf-apex and blades usually less than twice as long as wide.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 147. CLETHRACEAE[1]

BY KENNETH R. ROBERTSON
Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

Shrubs or small trees with stellate pubescence or rarely glabrous. *Leaves* simple, alternate, the margin entire or toothed. *Inflorescences* racemose or paniculate, terminal, bracts deciduous. *Flowers* ☿, actinomorphic, white or pinkish, fragrant, usually nodding; sepals 5, united at extreme base, imbricate, persistant around fruit; petals 5, distinct, imbricate, deciduous, larger than sepals, emarginate at apex; stamens 10 rarely 12, distinct, in two whorls, the filaments slender, subulate or flattened, the anthers sagittate, extrorsely inflexed in bud, becoming inverted and introrse at anthesis, opening by apical pores; pollen grains not in tetrads, 3-colporate; disc obsolete; ovary superior, globose to transversely-elliptic, pubescent, 3-lobed, 3-locular, the ovules numerous, borne on axile placental intrusions, anatropus, the style 1, erect, persistant on fruit, the stigma 3-lobed. *Fruit* capsular, subglobose, pubescent, 3-lobed, loculicidally 3-valvate, the valves 2-cleft; seeds numerous, compressed or trigonous, sometimes winged, the seed coat thin, the endosperm fleshy, the embryo cylindrical, short. The family contains only the genus *Clethra*. *Schizocardia* was described and placed in this family by Smith & Standley (Trop. Woods **32:** 8, 1932) but Thomas (Jour. Arnold Arb. **42:** 110-111, 1961) placed it in synonomy with *Purdiaea* of the *Cyrillaceae*.

CLETHRA

Clethra L., Sp. Pl. 396, 1753.

Characters of the family.

A genus of 20-25 species in tropical and sub-tropical Asia and America and in the Madeira Islands. The greatest area of diversification is in tropical America. Britton (N. Amer. Fl. **29:** 5, 1914) recognized 21 species in North America with 12 found in Mexico and Central America and one in Panama.

1. **Clethra lanata** Mart. & Gal., Bull. Acad. Brux. **9**(1): 538, 1842.—Fig. 1.

C. costaricensis Britton, N. Amer. Fl. **29:** 5, 1914.
C. panamensis Standley & Williams, Ceiba **1:** 160, 1950 .

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

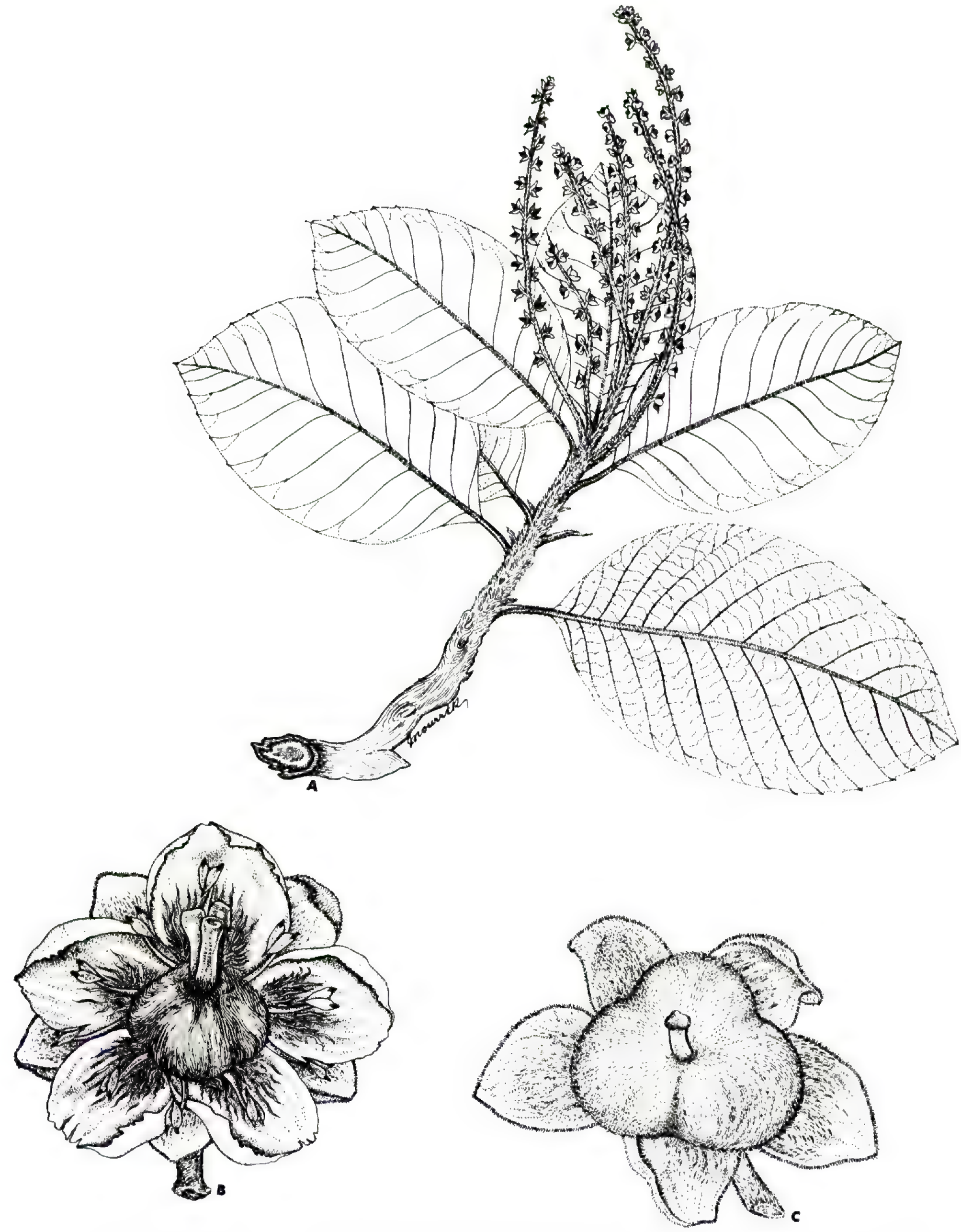

Fig. 1. *Clethra lanata* Mart. & Gal.: A, habit (× 4/9); B, flower (× 6); C, fruit (× 7). A after *Tyson 3714* (MO); B after *White 57* (MO); C after *Lewis et al. 1628* (MO).

Trees or sometimes shrubby, 2-30 m tall, sometimes buttressed at base; young branches, petioles, and bases of peduncles densely rusty-brown lanate. *Leaves* grouped toward the tips of branchlets with smaller young leaves at the apices; blades of mature leaves obovate, elliptic-obovate or oblong-obovate, 7-18 cm long, 3-9 cm wide, chartaceous to sub-coriaceous, obtuse or acute at apex, narrowed at the base, the margin entire to slightly denticulate due to the emergence of the veins from the leaf blade, the midrib prominent below, scattered stellate or simple pubescence above, denser in vein furrows, below somewhat paler with two types of pubescence, one short, stellate, and forming a layer covering entire lower surface, the other long, simple or stellate, and confined to the veins and veinlets, either layer may be absent on some individuals; petioles stout, up to 2 cm long. *Inflorescences* many flowered, 4-10 simple or branched fasiculate racemes, 8-26 cm long, the upper part of peduncle and pedicels pale, densely tomentose, the pedicels 2.5-7 mm long. *Flowers* white, very sweetly aromatic; sepals 5, ovate, 3-5 mm long, puberulent-tomentose within, tomentose without; petals 5, obovate, short-fimbricate, slightly longer than the sepals, pilose within, glabrous without; stamens 5, filaments subulate, glabrous, the anthers sagittate; ovary transversely-elliptic, densely pilose, the style 1.5-2.5 mm long, the stigma 3-lobed, lobes spreading. *Capsule* transversely-elliptic, pilose to tomentose, to 6 mm in diam; seeds 3, compressed.

A variable species distributed from Oaxaca to Panama. Found in the mountainous regions of western Panama as low as 400 m (*Lewis et al. 1628*), but more commonly found at elevations of 1000-2000 m and often in rather arid habitats.

CHIRIQUÍ: llanos on slopes of Volcán de Chiriquí Viejo & along Río Chiriquí Viejo, alt 1200 m, *Allen 999* (NY, US); vic of Cerro Punta, alt 2000 m, *Allen 1515* (MO, NY, US); llano del Volcán, alt 1500 m, *Allen 3501* (MO, NY, US); Bajo Mono, Boquete District, *Davidson 581* (MO); Cerro Horqueta, alt ca 1500 m, *Duke et al. 13618* (MO); forest of Cerro de Lino, above El Boquete, alt 1300-1500 m, *Pittier 3031* (US); forests around El Boquete, alt 1000-1300 m, *Pittier* 3322 (NY, US); vic of Boquete, Llanos Francia, alt 3300 ft, *Stern et al. 1165* (MO); 5 mi NE of El Volcán, alt ca 6300-6500 ft, *Tyson 805* (MO); Río Chiriquí Viejo valley, on llanos nr Cantina, *White* 57 (MO, US); valley of the upper Río Chiriquí Viejo, *White & White 93* (MO), *White* 333 (MO, NY, US); Finca Lérida to Boquete, alt ca 1300-1700 m, *Woodson et al. 1114* (MO, NY). COCLÉ: hills S of El Valle de Antón, alt 1000 m, *Allen 2508* (US); cloud forest on slopes of Cerro Pilon nr El Valle, alt 700-900 m, *Duke 12106* (MO). HERRERA: 12.5 mi S of Ocú, alt 1200 ft, *Lewis et al. 1628* (MO); vic of Las Minas, La Peña, *Stern et al. 1750* (MO). PANAMA: vic of Cerro Jefe, alt 600 m, *Allen 3437* (holotype of *C. panamensis* US; isotypes MO, NY); dry slopes of Campana Hill, vic of Campana, alt ca 600 m, *Allen 2438* (NY); along dry roadside, Cerro Campana, *Blum & Miller 2285* (MO); vic of Goofy Lake, *Blum et al. 2268* (MO); along rd toward top of Cerro Campana, *Duke 6022* (MO); area nr Carretera Transisthmica several mi N of its intersection with Madden Rd, *Stimson 5123* (MO); W slope of Cerro Campana, *Tyson 4042* (MO). VERAGUAS: 2 mi S of Canazas, *Tyson 3714* (MO).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 159. LOGANIACEAE[1]

BY WILL H. BLACKWELL, JR.
Missouri Botanical Garden, St. Louis, Missouri

Herbs, shrubs, trees or lianas, milky latex absent. *Leaves* opposite, simple, stipulate (stipules sometimes reduced to stipular lines). *Inflorescences* basically cymose though often much modified (solitary flowers, spiciform inflorescences, thyrses, etc.). *Flowers* ☿ or less frequently functionally ♂ ♀, actinomorphic, 4- or 5-merous (the corolla and stamens rarely pleiomerous); calyx-lobes imbricate; corolla sympetalous, the lobes with valvate, imbricate or contorted aestivation; stamens epipetalous, alternate with the corolla-lobes; nectariferous disc absent or small; ovary superior (rarely ½ inferior), 2-carpellate and 2-locular (rarely 1-or 4-locular), the ovules several to ∞ per locule, amphitropous or anatropous, the placentation axial (parietal in 1-locular ovaries), the style terminal, usually simple, with a capitate or 2-lobed stigma (occasionally the stigmatic region scarcely apparent). *Fruit* a capsule, drupe or berry; seeds usually small, winged or exalate, possessing endosperm, the embryo straight.

A family of 33 genera and about 600 species, mainly tropical; five genera are known to occur in Panama, a sixth is suspected.

a. Fruits baccate and indehiscent; leaf-blades 3-5-plinerved or if pinnately nerved then 30 cm or more in length.
  b. Leaf-blades pinnately nerved, 30 cm or more in length, frequently oblanceolate or obovate; corolla-lobes and stamens 10; corolla-lobes strongly imbricate in the bud; staminal filaments connate by a membranous sheath .....4. *Potalia*
  bb. Leaf-blades typically 3-5-plinerved, less than 30 cm in length; corolla-lobes and stamens 4 or 5; corolla-lobes valvate in the bud; staminal filaments absent or not connate .....5. *Strychnos*

aa. Fruits capsular and dehiscent; leaf-blades usually pinnately nerved (rarely with the secondaries obscure) and less than 30 cm long.
  c. Flowers secund in simple or dichotomous spikes or smaller cincinnous clusters; capsules dehiscing circumscissilly and leaving a cupular base or else deeply 2-lobed apically (frequently for ½ or more of the capsule length), the lobes often spreading at maturity.
    d. Leaves often quaternate or pseudo-quaternate at the apical node (sometimes opposite); spikes simple or occasionally irregularly branched; capsules splitting open by 4 valves and then dehiscing circumscissilly to leave a cupular base in the persistent calyx; corolla funnelform or tubular-funnelform, the tube considerably exceeding

[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

2 mm in length .....1. *Spigelia*

dd. Leaves opposite at all nodes; spikes or cincinnous inflorescences dichotomous; capsules not circumscissilly dehiscent, deeply 2-lobed apically, the lobes deshiscing vertically along their interior margins; corolla urceolate, the tube usually not exceeding 2 mm in length .....2. *Cynoctonum*

cc. Flowers not secund in simple or dichotomous spikes; capsules neither dehiscing circumscissilly nor deeply 2-lobed.

e. Herbs, prostrate or matted; leaf-blades 3 mm broad or less; flowers solitary in axils of branches and leaves; calyx-tube shorter than the calyx-lobes; calyx and corolla without stellate trichomes ....6. *Polypremum*

ee. Shrubs or trees; leaf-blades more than 3 mm broad; inflorescences several to ∞-flowered; calyx-tube equal to or longer than the calyx-lobes; calyx and corolla covered externally with stellate trichomes .....3. *Buddleia*

1. SPIGELIA

Spigelia L., Sp. Pl. 149, 1753; Gen. Pl. ed. 5, 74, 1754.

Herbs (annual or perennial) or suffrutices, glabrous or pubescent with simple or stellate trichomes. *Leaves* opposite, often in a whorl or pseudo-whorl at the stem apex, connected by interpetiolar lines or sheaths or stipules; blades simple, most often membranous, usually pinnately nerved. *Inflorescences* spicate, terminal. *Flowers* ☿, secund, the pedicels reduced or absent; calyx-lobes 5, often slender, free or connate at the base, equal or unequal, persisting after the dehiscence of the capsule; corolla usually funnelform, delicate, the lobes 5, valvate in bud, shorter than the tube; stamens 5, the anthers included or exserted, the filaments not connate, attached to the corolla-tube; ovary 2-locular with several ovules per locule, the style slender, unbranched, grading almost imperceptibly into the stigma, the stigma not manifestly swollen, eventually articulating at the middle or somewhat above (thus with at least the lower ½ persisting). *Fruit* a didymous capsule opening by 4 valves (loculicidally and septicidally), subsequently dehiscing circumscissilly above a persistent cupular base (the valves thus deciduous), the often ± ellipsoidal cupular base centrally foveate; seeds subglobose or ovoid, sometimes subangulate by mutual pressure, tuberculate or scabrous or reticulate on the surface.

A New World genus of about 50 species centered in South America but with some temperate representatives; one species (*S. anthelmia* L.) has become naturalized in parts of Africa; as interpreted in this paper, two species occur in Panama.

a. Spikes often 2-5 at the stem or branch apices (occasionally solitary); calyx-lobes minutely ciliate marginally, often unequal; capsules conspicuously muricate externally, the persistent cupular base pointed at the ends .....1. *S. anthelmia*

aa. Spikes typically solitary at the stem or branch apices (rarely 2); calyx-lobes usually entirely glabrous, ± equal; capsules smooth externally, the persistent cupular base rounded to truncate or emarginate at the ends .....2. *S. humboldtiana*

1. **Spigelia anthelmia** L., Sp. Pl. 149, 1753.—Fig. 1.

S. multispica Steudel, Flora **26**: 764, 1843.
S. killipii Ewan, Caldasia **4**: 302, 1947.

Herb, annual, 15 cm-1.3 m high, the roots usually shallow and fibrous; stems ascending, leafless below the apical leaf whorl (the apical whorl actually consists

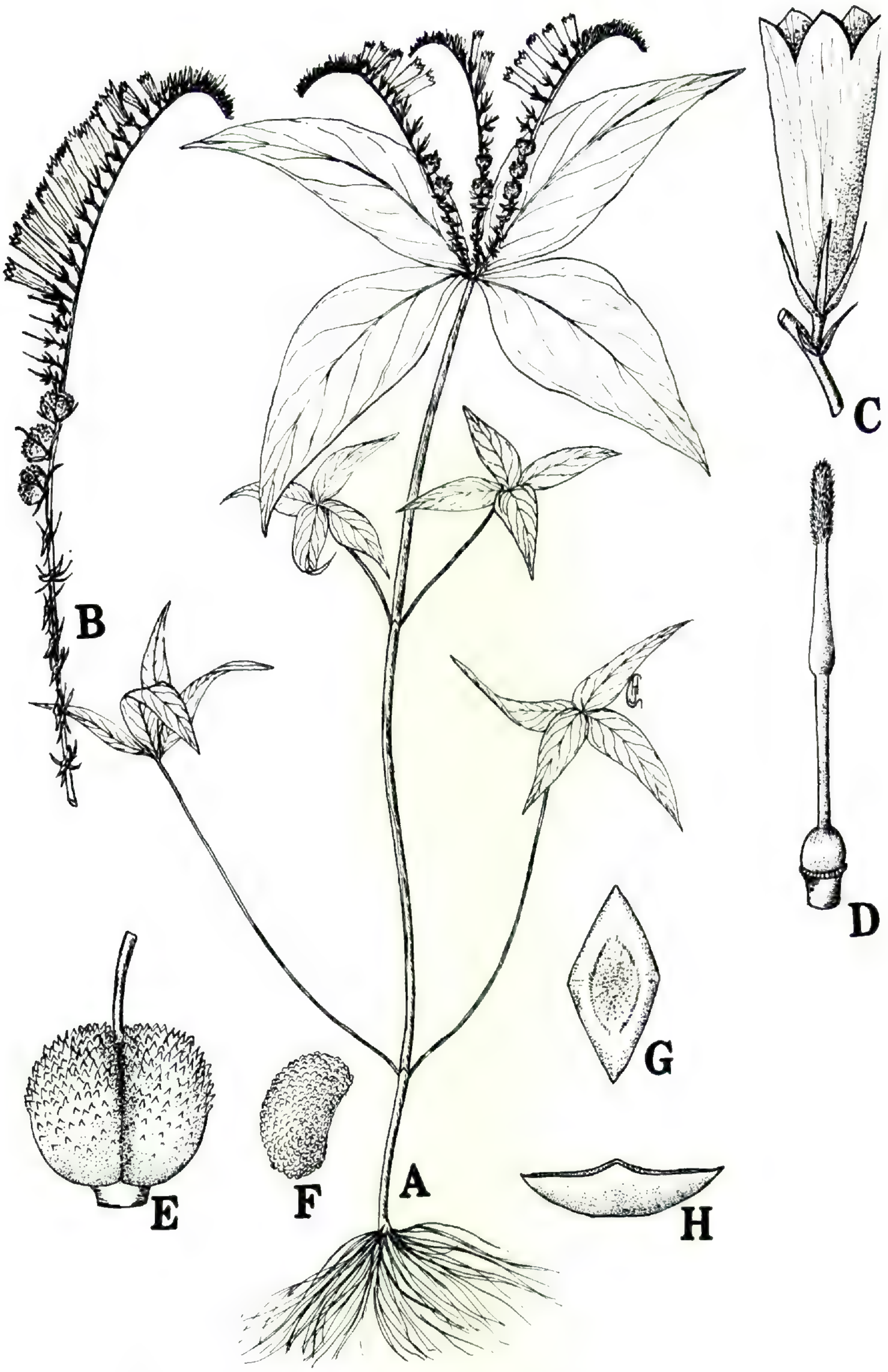

Fig. 1. *Spigelia anthelmia* L.: A, habit (×½); B, spike (×1); C, flower (×3); D, pistil (×5); E, capsule (×5); F, seed (×10); G-H, persistent cupular base of capsule (×7). A after *Stern et al. 70* (MO); B-D after *Woodson et al. 1674* (MO); E-H after *Lundell 4987* (MO), Mexico.

of 2 decussate and sometimes unequal leaf-pairs not separated by a manifest internodal area) or with 1-2 cauline leaf-pairs reduced in size with respect to the apical whorl, simple or few-branched, glabrous or puberulent on the extreme distal portion with simple trichomes 0.1 mm long or less, becoming ± terete and suffrutescent at the base; branches and at least the distal ½ of the main stem compressed, green, weak, subsucculent, often faintly striolate. *Leaves* sessile or with petioles to 10(-20) mm long, the leaves of the terminal whorl often sessile or subsessile; blades 2-18 cm long, 0.8-6.5 cm broad, broadly ovate or rhombic-ovate to lance-oblong or lance-elliptic or lanceolate, apically acuminate or acute, basally acute to broadly rounded or sometimes approaching subtruncate, often decurrent long the petiole, paler green below, membranous, marginally usually ciliate with simple mammillate trichomes 0.1 mm long or less, glabrous above or with minute scattered mammillate trichomes, glabrous below or minutely puberulent along the main veins, the midvein and secondaries apparent on both surfaces, sometimes slightly raised below, the 6-14 secondaries arising pinnately from the midvein and arcuate-ascending, the reticulation typically faint or obscure on both surfaces; stipules broadly deltoid, 1-3 mm long. *Spikes* 1-5, simple or infrequently branched, 3-18 cm long, 10 to 40-flowered, terminal but sometimes overtopped by floriferous branches. *Flowers* closely aggregated at the tip of the spike, soon separated by 2-7(-15) mm by internodal elongation, the pedicels obsolete to 1 mm long; calyx-lobes free to the base, linear-lanceolate, often dialated at the base, 2-6.5 mm long, unequal or subequal, minutely ciliate marginally and externally along the keeled midrib but otherwise glabrous; corolla rather narrowly funnelform or tubular-funnelform, white to pink or lavender, glabrous, soon fugaceous, the tube 6-16 mm long, 2-4.5 mm broad at the throat, 0.7-1.5 mm broad at the base, the lobes ovate-deltoid or virtually rhombic, 2-3 mm long; anthers included, 0.8-1.5 mm long, the free-portion of filaments ca 2 mm long, attached to corolla-tube somewhat above the middle; ovary ca 0.8 mm long, subglobose, the style extending to the opening of the corolla-throat, with the upper ½ (or slightly less) swollen and eventually deciduous, the stigmatic region pubescent. *Capsules* ca 4 mm long, 5-6 mm broad, compressed at right angles to the septum, conspicuously muricate except at the base, the persistent cupular base navicular, pointed at the ends; seeds brownish, ovoid to suborbicular, 1.5-2 mm long, carnose, externally conspicuously tuberculate.

Tropical America, from Mexico and Florida to Peru and Brazil; naturalized in tropical Africa (especially West Africa) and Indonesia.

BOCAS DEL TORO: Changuinola to 5 mi S at junction of Ríos Changuinola & Terebé, *Lewis et al. 913* (MO); vic of Chiriquí Lagoon, Fish Creek, *von Wedel 2228* (MO). CANAL ZONE: nr mouth of Río Chagres, *Allen 902* (MO, US); Barro Colorado I, *Bailey & Bailey 367* (F), *Ebinger 614* (MO), *Shattuck 1126* (F), *1171* (F, MO), *Tyson 4202* (MO); Mojinga Swamp, *Bailey & Bailey 584* (F); vic of Cerro Viejo on K164, *Blum 1254* (MO); Galena point, *Blum & Dwyer 2143* (MO); Fort Kobbe, *Duke 3967* (MO); Miraflores Bridge, *Dwyer 1008* (F); Chagres, *Fendler 283* (MO, US); Pedro Miguel, *Bro. Heriberto 90* (US); Ancon, *Killip 3328* (US), *12109* (US); Balboa, *Standley 25495* (US), *30899* (US); Corozal, *Standley 27389* (US); Río Pedro Miguel, nr East Paraíso, *Standley 29926* (US); vic of Balboa, western slope of Ancon Hill, *Seibert 112* (F, MO); vic of Miraflores Locks, *Stern et al. 70* (MO); Fort Sherman, *Tyson & Blum 1672* (MO), Summit Garden, *Tyson & Blum 1990* (MO); Gamboa, *Tyson et al. 4569* (MO). CHIRIQUÍ: David airport, *Lewis et al. 736*

(MO). COLÓN: Nuevo Chagres, *Lewis et al. 1864* (MO). DARIEN: vic of Pinogana, *Allen 929* (F, MO, US); Mt Pirri, *Goldman 1962* (US); vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 812* (MO, US). LOS SANTOS: 3 mi S of Carreta, ca 5 mi S of Las Tablas, *Burch et al. 1228* (MO). PANAMA: nr beach at Nueva Gorgona, *Duke 4497* (MO); Río Pita, 1-3 mi above confluence with Río Maestra, *Duke 4761* (MO); San José I, *Erlanson 435* (US); Juan Díaz, *Killip 3120* (US); Taboga I, *Pittier 3624* (US), *Woodson et al. 1451* (F, MO); Laguna de Juan Corso, nr Chepo, *Pittier 4669* (US); vic of Juan Franco Race Track, nr Panama, *Standley 27745* (US); thickets & forests nr Arraiján, *Woodson et al. 1674* (MO). SAN BLAS: Mulatuppu, Río Ibedi, *Duke 8460* (MO); Aligandi, mainland, *Dwyer 6811* (MO); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi inland, *Lewis et al. 78* (MO). VERAGUAS: Isla de Uva, Contreras group, *Pittier 5107* (US).

Spigelia killipii is distinguished from *S. anthelmia* by Ewan (Caldasia **4:** 294, 1947), in his key to species, by the leaves of the apical whorl which are distinctly petiolate and not conspicuously verticillate. The type specimen (*Killip 35101*, US) from Colombia and an additional specimen from Panama (*Killip 3120*, US) cited by Ewan were examined. Leaves of the apical whorl present on the stem and branches of both specimens were found to be verticillate or essentially so. The distinctive petioles of the type specimen are much reduced in *Killip 3120*. The rather striking pubescence of the distal portion of the stem and branches of the type specimen is not evident on *Killip 3120*. *Spigelia killipii* is probably best regarded as conspecific with *S. anthelmia*, the type specimen being a rather aberrant individual.

2. **Spigelia humboldtiana** Cham. & Schlecht., Linnaea **1:** 200, 1826.

S. scabra Cham. & Schlecht., loc. cit. 202.
S. palmeri Rose, Contr. U.S. Nat. Herb. **1:** 342, 1895.

Herb or low suffrutex 1-6 dm high, the roots usually fibrous; stems slender, simple or branched, glabrous or rather sparsely pilose distally in strips down each side (often along the margins of sulcae), the proximal portion often creeping. *Leaves* at the apex whorled, imperfectly whorled, or opposite, additional cauline leaf-pairs usually present; blades lance-ovate or lance-elliptic, infrequently lanceolate or narrowly elliptic-lanceolate, apically acute or subacuminate, basally cuneate to subtruncate or rounded, often decurrent along the petiole, 2-10 cm long, 0.8-4.5 cm broad, membranous, glabrous or with scattered pilose or mammillate trichomes above, occasionally minutely puberulent below on the main veins; petioles extremely variable, obsolete to 15 mm long. *Spikes* 1(2), terminal, usually simple, 3-13 cm long, 6-35-flowered, occasionally overtopped by floriferous branches. *Flowers* with pedicels obsolete to 1 mm long; calyx-lobes glabrous or glabrate, subulate, free to the base, equal or subequal, 2-4 mm long; corolla slender-funnelform (sometimes rather abruptly expanded above), white, often tinged with pink, glabrous, the tube 9-19 mm long, 1 mm broad at the base, 3-7.5 mm broad at the neck, the lobes ovate or deltoid-ovate, 3-4 mm long; anthers well-included, 1-1.5 mm long, very slender, the free-portion of filaments ca 2 mm long, attached to the corolla-tube above the middle; style included (the tip extending to or just beyond the location of the anthers), puberulent on the upper portion, approximately the upper

½ enlarged and deciduous. *Capsules* smooth externally (not muricate), 4-6 mm broad, 2.5-4 mm long, the persistent cupular base rounded to truncate or emarginate at each end, centrally foveate; seeds brownish, ovoid, carnose, ca 1.5 mm long, often reticulate or tuberculate on the surface.

Northern Mexico to Argentina.

BOCAS DEL TORO: region of Almirante, *Cooper 100* (F), *152* (F), *180* (F); Changuinola Valley, *Dunlap 237* (F); Changuinola to 5 mi S at junction of Ríos Changuinola & Terebé, *Lewis et al. 912* (MO); Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1957* (MO); vic of Chiriquí Lagoon, Water Valley, *von Wedel 746* (MO), *1725* (MO); vic of Chiriquí Lagoon, Old Bank I, *von Wedel 2004* (MO); vic of Chiriquí Lagoon, Fish Creek Mts, *von Wedel 2348* (MO, US); vic of Nievecita, *Woodson et al. 1808* (MO). CANAL ZONE: Barro Colorado I, *Ebinger 23* (MO), *552* (MO), *Hayden 25* (MO), *Shattuck 1165* (F, MO), *Starry 86* (F); Gatuncillo River, *Rowlee & Rowlee 417* (US); hills N of Frijoles, *Standley 27564* (US). CHIRIQUÍ: Boquete, *Davidson 654* (F, MO); forests around El Boquete, *Pittier 3291* (US); vic of San Bartolomé, Peninsula de Burica, *Woodson & Schery 928* (MO); Finca Lérida to Boquete, *Woodson et al 1146* (F, MO). COCLÉ: 12 mi NE of Penonomé, *Lewis et al. 1527* (MO). DARIEN: vic of Yape, *Allen 862* (F, MO, US); headwaters of Río Chico, *Allen 4605* (MO). PANAMA: Capira, *Bro. Maurice 807* (US); Río Tapia, *Standley 26143* (US). SAN BLAS: mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi inland, *Lewis et al. 205* (MO).

Photographs (F, US) showed type material of *S. humboldtiana* and *S. scabra* to belong to one taxon. As either name may be chosen as the specific epithet, I favor *S. humboldtiana* as it is better typified (based on the selection of a lectotype, *Humboldt & Bonpland 174*, by Ewan, loc. cit. 295).

2. CYNOCTONUM

Cynoctonum Gmelin in L., Syst. Nat. ed. 13, 443, 1791.

Mitreola R. Br., Prodr. 450, 1810.

Herbs or suffrutices, annuals (most) or low perennials; stems much branched to simple, glabrous or obscurely and minutely puberulent. *Leaves* opposite, distinctly petiolate to sessile or essentially so; blades typically ovate-lanceolate or elliptic-lanceolate but varying from virtually linear to broadly ovate or suborbicular, membranous or less frequently subcoriaceous, marginally entire. *Flowers* ☿, arranged unilaterally in terminal or axillary dichotomizing spikes or smaller cincinnous clusters, the pedicels not exceeding 1 mm in length; calyx-lobes 5, lanceolate or ovate-lanceolate, basally imbricate in bud, longer than the tube, persistent in fruit; corolla urceolate, white or less frequently pink, fugaceous as a unit, the tube somewhat swollen, 0.7-2 mm long, contracted at the throat, with a dense ring of villous trichomes in the throat ca 0.5 mm long, the lobes 5, 0.5-2 mm long, valvate in bud, slender-lanceolate to ovate, ascending to suberect but arcuate and with the tips incurved; anthers 5, ovate, basally cordate, 0.3-0.5 mm long, included, attached to the corolla-tube half way between the middle and the base by filaments with the free-portions slightly longer than the anthers; ovary subglobose or turbinate, ½ inferior, 0.7-1 mm long, 2-locular, with ∞ ovules per locule, the separate carpel apices apparent in mature flowers, the styles 2, less than ½ the ovary length, united above by a small capitate stigma, splitting apart as the fruit develops.

Capsules 2-4 mm long, sparsely to moderately covered with minute hispidulous trichomes or with small papillations, deeply 2-lobed, the capsule-lobes frequently comprising ½ or more of the capsule length, spreading apart by 10-120° at maturity, with the tips straight or curving inward to various degrees, dehiscing vertically along the inner margin; seeds ovoid, brownish, glossy, 0.3-0.5 mm long, furrowed on one side.

A genus of three or four species distributed in temperate and tropic regions of the New World; only one species is known to occur in Panama.

1. **Cynoctonum mitreola** (L.) Britton, Mem. Torrey Bot. Club **5:** 258, 1894.—Fig. 2.

Ophiorrhiza mitreola L., Sp. Pl. 150, 1753.
Cynoctonum petiolatum Gmelin in L., Syst. Nat. ed. 13, 443, 1791.
Mitreola petiolata (Gmelin) Torrey & Gray, Fl. N. Amer. **2:** 45, 1846.

Herb or suffrutex to 1 m high; branches opposite, slender, distally compressed, often canaliculate, the younger branches green, the older brown or grayish-brown. *Leaves* with petioles 1.5-25 mm long; blades usually ovate-lanceolate or elliptic-lanceolate, apically acute or subacuminate, basally cuneate or occasionally subtruncate, often decurrent along the petiole, 1.5-9.6 cm long, 0.7-4.3 cm broad, the margins ciliate with simple bulbous trichomes 0.05-0.2 mm long, the upper and lower surface glabrous or with a puberulence similar to that of the margins (often confined to the main veins), the midvein evident but usually not conspicuously raised on either surface (occasionally somewhat raised below), the 6-20 secondaries pinnate and arcuate-ascending.

Occurring sporadically from the southeastern United States to northern South America and the West Indies.

CANAL ZONE: Cocoli rd, *Burch et al. 1401* (MO); Río Grande, nr Culebra, *Pittier 2099* (US); Balboa, *Standley 25253* (US), *25479* (US), *26434* (US); Gamboa, *Standley 28519* (US); along the old Las Cruces Trail, betw Fort Clayton & Corozal, *Standley 29150* (US); vic of Fort Sherman, *Standley 30971* (US); vic of Miraflores Lake, *White 273* (F, MO). HERRERA: 4 mi S of Los Pozos, *Tyson 2671* (MO). PANAMA: hills betw Capira & Potrero, *Dodge & Hunter 8628* (MO); Sabanas nr Chepo, *Hunter & Allen 59* (MO, US); Agricultural Experiment Station at Matías Hernández, *Pittier 6881* (US), *6891* (US); nr Punta Paitilla, *Standley 26239* (US); along the Corozal Rd, nr Panama, *Standley 26825* (US); Río Tapia, *Standley 28119* (US); nr Matías Hernández, *Standley 28932* (US); Río Tocumen, *Standley 29466* (US); betw Las Sabanas & Matías Hernández, *Standley 31900* (US). LOS SANTOS: ca 5 mi S of Las Tablas, *Burch et al. 1275* (MO).

The 2-lobed capsule of this species resembles a bishop's miter and accounts for the often used common name miterpod. The distinctive nature of the capsule permits ready identification of fruiting material in the field, as attested by the high percentage of collected specimens which are in fruiting condition.

The three varieties proposed by Hochreutiner (Bull. N. Y. Bot. Gard. **6:** 284, 1910) based on the degree of curvature of the capsule-lobes are not recognized, as much of the variation assigned to these suggested segregates may be observed on a single specimen.

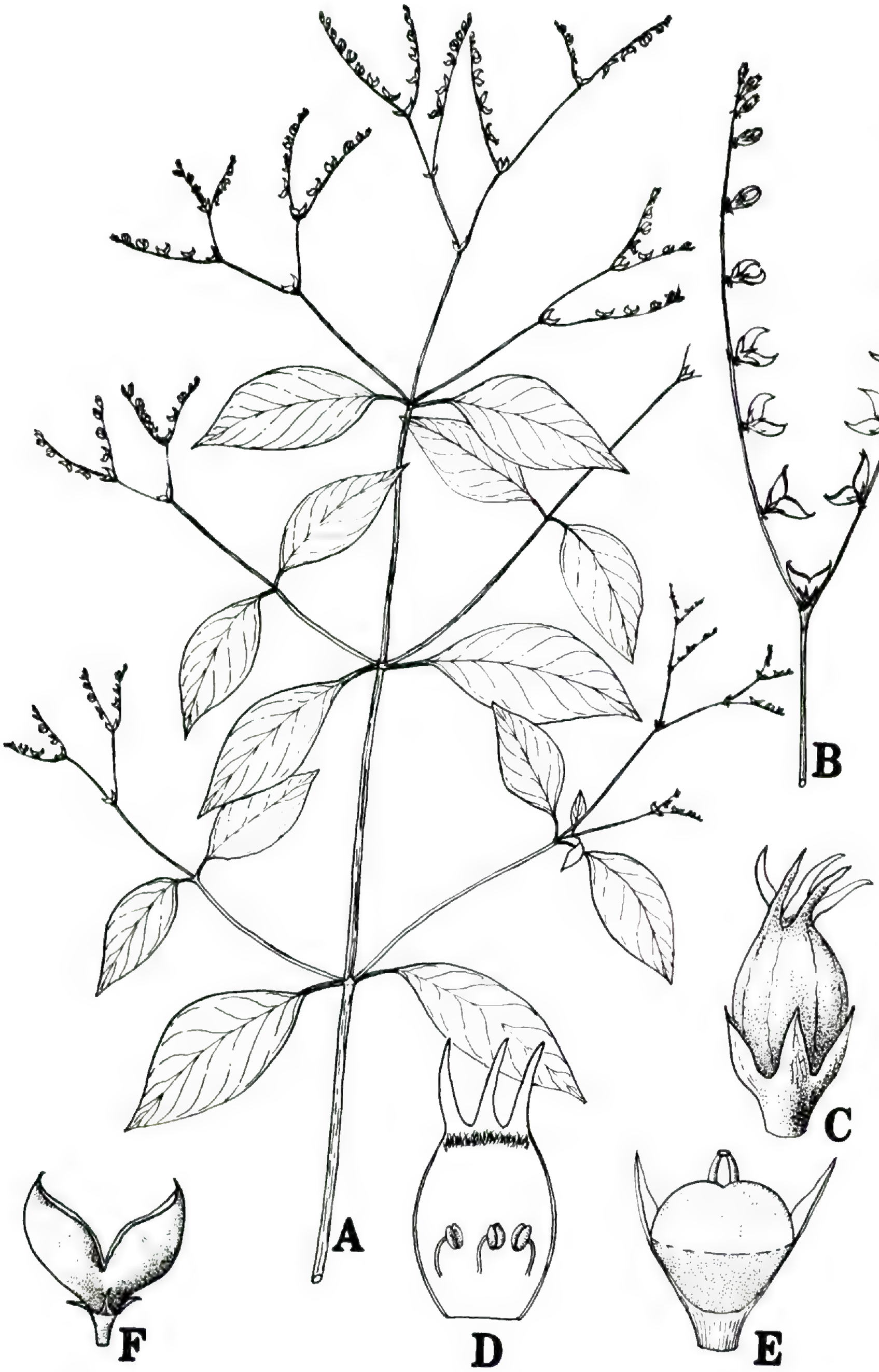

Fig. 2. *Cynoctonum mitreola* (L.) Britton: A, habit (×½); B, dichotomous branch of inflorescence with fruit developing toward base (×2); C, flower (×13); D, internal view of portion of corolla showing attachment of stamens (×15); E, flower with corolla and stamens removed (×20); F, capsule (×6). After *Burch et al. 1401* (MO).

3. BUDDLEIA

Buddleia L., Sp. 112, 1753; Gen. Pl. ed. 5, 51, 1754. (*Buddleja*)

Trees or shrubs; young branchlets conspicuously vested with stellate trichomes, frequently tetragonal; older branches glabrate, soon becoming woody and developing furrowed bark at the surface. *Leaves* simple, typically decussate, petiolate or sessile, with only a stipular line connecting the petioles (rarely with well developed foliaceous stipules); blades variable in size and shape, pinnately nerved, the lower surface conspicuously pubescent with stellate trichomes, often also with smaller glandular trichomes underlying the stellate pubescence, the upper surface more sparsely pubescent or sometimes glabrous. *Inflorescences* basically paniculate but varying from a rather loose, terminal panicle with ultimate dichasial units to a racemose series of cymules (sometimes pseudoverticillate in appearance) or a compact head. *Flowers* usually rather small, actinomorphic, often functionally ♂ ♀ (the sterile organ or organs sometimes poorly developed); calyx green, usually covered with a stellate tomentum, the 4 lobes usually shorter than (sometimes equal to) the tube, persistent in fruit; corolla yellow, orange or white (pink or purple in some oriental and African species), campanulate, funnelform or salverform, covered externally with stellate trichomes, internally with simple unicellular (and pitted) hairs which are distributed variously, the lobes 4, valvate or imbricate, usually shorter than the tube; stamens 4, inserted on the upper ½ of the corolla-tube; ovary ovoid or subglobose, 2-locular, the number of ovules per locule variable, the style single, short, usually not extending appreciably beyond the corolla-lobes, the stigma clavate, usually notched at the apex. *Capsules* ovoid to oblong, less frequently subglobose, dehiscing septicidally, subsequently splitting loculicidally but only at the apex; seeds not exceeding 1.5 mm in length, ovate to oblong or slender and elongate, winged or wingless.

A genus of about 140 species with representatives occurring in southern Asia, Africa, and North and South America. The greatest concentration of species is South American but numerous Old World representatives occur; two species are native to Panama.

Useful reference:

Norman, E. M., The genus *Buddleia* in North America. Gentes Herbarum **10:** 47-116, 1967.

a. Leaf-blades subcoriaceous, entire, appressed-puberulent beneath with stellate trichomes less than 0.3 mm broad; calyx-tube ca twice as long as the calyx-lobes; corolla-lobes imbricate in the bud, internally with the unbranched trichomes not organized into a crescent-shaped band .....1. *B. nitida*

aa. Leaf-blades membranaceous, serrate or serrulate (sometimes entire), rather loosely pubescent beneath with stellate trichomes 0.4-1 mm broad; calyx-tube ca equaling the calyx-lobes; corolla-lobes valvate in the bud, internally with the unbranched trichomes forming a conspicuous crescent-shaped band .....2. *B. americana*

1. **Buddleia nitida** Bentham in DC., Prodr. **10:** 437, 1846.

B. alpina Oersted, Vid. Medd. Nat. For. Kjöbenh. **1853:** 25, 1853.

Shrub or small tree 3-10 m high; youngest branchlets with a closely appressed puberulence of minute stellate trichomes ca 0.1-0.2 mm broad, soon glabrous, the

internodes 0.5-2(-3.5) cm long; older branches developing gray or grayish-brown bark. *Leaves* with petioles 3-22 mm long which are connected by stipular lines; blades oblong-lanceolate, 2.3-8 cm long, 0.6-2.6 cm broad, apically acute or attenuate, basally cuneate to rounded, subcoriaceous, densely appressed-puberulent beneath with stellate trichomes 0.1-0.2 mm broad, glabrous or with a few scattered stellate trichomes above, the midvein raised beneath, the secondaries 8-20 in number, usually apparent (at least below), not arcuate, anastomosing marginally, the tertiaries usually obscure above and below. *Inflorescences* paniculate, 2-8 cm long, with 3 or sometimes 4 orders of branching, the ultimate units small 3-flowered dichasia which are subsessile or short-pedunculate. *Flowers* with pedicels 0-1 mm long; calyx funnelform or campanulate, stellate-tomentellous externally, the tube 1-2.5 mm long, the lobes deltoid, 0.5-1 mm long; corolla funnelform, stellate-tomentellous externally, internally with unbranched pitted trichomes ca 0.5 mm long randomly dispersed on the lower ⅔ of the lobes and the upper ⅓ of the tube, the tube 2.5-3 mm long, the lobes ovate, 1-2 mm long, imbricate in bud; anthers 0.7-1 mm long, the filaments becoming free from the corolla-tube near the middle or almost at the throat, the free-portion ca 0.5 mm long; ovary subglobose to ovoid, 1-1.5 mm long, externally appressed-stellate-puberulent, the ovules ∞ per locule, the placenta a central column 0.7-1 mm broad often remaining attached basally after the seeds are shed, the style ca 1 mm long, the stigma 1 mm long, minutely retuse. *Capsules* narrowly ovoid or subcylindrical, 4-5.5 mm long.

According to Norman (loc. cit. 75), *B. nitida is* "a common tree of the sierras of southern Chiapas to Panama."

CHIRIQUÍ: Llano del Volcán, *Allen 3458* (F, MO, US); summit & SW face of Cerro Copete, *Allen 4880* (F, MO); El Boquete, Volcán de Chiriquí, *Davidson 947* (F, MO, US), *1313* (F, MO); in deep canyon bottom, 5 mi NE of El Volcán, *Tyson 808* (MO); valley of the upper Rio Chiriquí Viejo, Cerro Pando, *White 47* (MO); Río Chiriquí Viejo valley, nr El Volcán, *White 202* (MO, US); Potrero Muleto to summit, Volcán de Chiriquí, *Woodson & Schery 419* (MO, US).

2. **Buddleia americana** L., Sp. Pl. 112, 1753.—Fig. 3.

Shrub or small tree 2-5(-10) m high, the new growth herbaceous and possessing a tomentum of grayish-white stellate trichomes, the older branches becoming glabrous and developing brownish bark. *Leaves* with petioles 2-20 mm long; blades quite variable in shape but generally lanceolate to broadly lance-ovate or lance-elliptic, membranous, apically acute or acuminate, basally attenuate to obtuse, often decurrent along the petiole basally, (3-)6-22 cm long, 1.8-9 cm broad, usually serrate or serrulate (infrequently entire), the lower surface with a rather loose vesture of stellate trichomes 0.4-1 mm broad underlaid by smaller glandular trichomes, the upper surface glabrous or with scattered stellate trichomes, the midvein raised beneath, the secondaries 8-18 in number, arcuate-ascending, anastomosing, the tertiaries reticulate, usually apparent. *Inflorescences* condensed-paniculate, 4.5-25 cm long, branching at the base, typically with only 1 or 2 orders of branching, the cymules compressed, subsessile or short-pedunculate, borne in

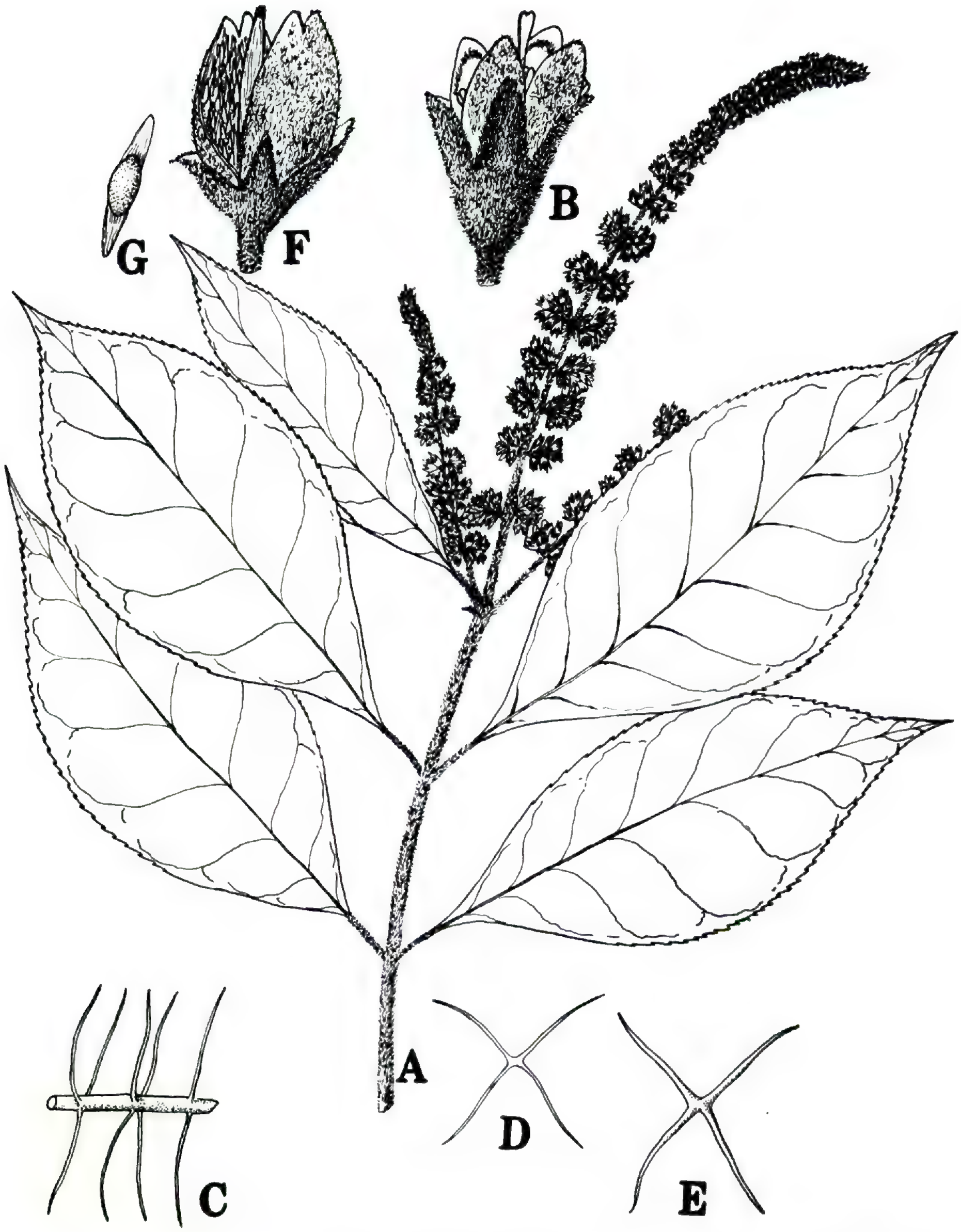

Fig. 3. *Buddleia americana* L.: A, habit (×½); B, flower (×7); C-E, stellate trichomes from distal portion of branch (×38); F, dehiscent capsule (×6); G, seed (×15). A-E after *Allen 967* (MO); F-G after *White 294* (MO).

a racemose and generally opposite fashion on the floriferous stalks, attaining a diam of 6-17 mm and containing 3-10 flowers. *Flowers* sessile or with pedicels to 1.5 mm; calyx funnelform-campanulate, externally stellate-pubescent, the tube 1.5-2.5 mm long, the lobes 1.3-2.5 mm long, lanceolate; corolla yellow or white, funnelform, stellate-pubescent externally, internally with a conspicuous V-shaped or cresent-shaped band of simple unicellular pitted trichomes on the lobes (the individual trichomes 0.4-1 mm long), glabrous in the tube, the tube 2-3 mm long, the lobes 2-3 mm long, lanceolate or slightly ovate-lanceolate, valvate in bud; anthers 0.7-1 mm long, narrowly ovate or oblong, the filaments adnate to the corolla-tube up to the throat, the free-portion less than 1 mm long; ovary 1.5-3 mm long, ovoid, externally stellate-pubescent, the ovules ∞ per locule, the style to 1 mm long, the stigma ca 1 mm long, apically emarginate, the placenta an axial column to 1 mm broad remaining attached basally after dehiscence of the capsule. *Capsules* narrowly ovoid or subcylindrical, 3.5-6 mm long; seeds slender-elongate, compressed, winged at each pole, 0.8-1.3 mm long.

In her monograph of the North American species of the genus *Buddleia*, Norman (loc. cit. 84) states that *B. americana* is the most widely distributed of the New World species. "Its range is from Tamaulipas in Mexico south through Central America and down the western coast of South America to Bolivia. It also includes the islands of Jamaica and Cuba." This species is known from a wide variety of habitats, including coastal lowlands and cloud forests.

CANAL ZONE: Cocoli I, vic of Miraflores Lake, *White 294* (MO). CHIRIQUÍ: llanos on slopes of Volcán de Chiriquí Viejo & along Río Chiriquí Viejo, *Allen 967* (MO); trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, *Allen 1470* (F, MO, US); El Boquete, Bajo Mono, *Davidson 458* (F, MO, US); forests around El Boquete, *Pittier 2888* (US); Chiriquí Viejo Valley, *White 105* (F, MO).

4. POTALIA

Potalia Aublet, Hist. Pl. Gui. Fr. 394, 1775.

Shrubs or small trees 0.3-5 m high, simple or sparingly branched. *Leaves* opposite; petioles 0.4-4 cm long, 2-7 mm broad, usually glabrous, connected by a short and truncate stipule-sheath; blades elongate-obovate or oblanceolate to oblong or anguste-elliptic, apically acuminate or subacuminate, basally acute to long-attenuate, 30-75 cm long, 7.5-18 cm broad, usually broadcast toward the apex or near the middle, simple, entire, glabrous, much darker green above than below, the midvein conspicuous and raised below, the secondaries typically more than 30, pinnate, alternate, arcuate-ascending, the reticulation faint or obscure on both surfaces. *Inflorescences* cymose-corymbose, solitary, terminal but often over-topped by lateral branches, several-flowered, with 1 or 2 orders of branching, the branches covered with a yellow granular powder which is readily shed.[2]

[2] Examination of the yellow granular powder covering the inflorescence-branches with the low power of a compound microscope revealed the ultimate granules to be minute, ornately branched or substellate trichomes. The true nature of these trichomes is not apparent without a compound miscroscope.

Flowers with pedicels 7-14 mm long and 2-3 mm broad; calyx-lobes 4 (the inner pair with margins overlapped by the outer pair), suborbicular to obovate, apically rounded, crassulate and coriaceous, membranaceous only at the margin, yellow, 5.5-8.5 mm long, a tube not apparent; corolla white to green or yellow, the tube short-campanulate and 2-3 mm long, the lobes 10, 4-6 mm long, ovate-lanceolate, basally auriculate, strongly imbricate, incurving at the tips; stamens 10, the anthers linear or slender-lanceolate, 4-5.5 mm long, the filaments connate by a membranaceous sheath ca 1 mm long which is attached near the base of the corolla-tube; ovary elevated on a fleshy disc to 1 mm long, ovoid, 2.5-4.5 mm long, the style 1 mm long or less, the stigma capitate and rather conspicuous. *Fruit* baccate, indehiscent, turbinate, ca 1.5-2 cm long and broad, 2-4 locular; seeds ∞, mostly oblong, brown, somewhat angular, 4-5.5 mm long, the testa pitted.

Potalia amara Aublet, Hist. Pl. Gui. Fr. 394, *pl. 151*, 1775.—Fig. 4.

The single species in the genus occurs from Brazil and Peru to Costa Rica; only a limited number of collections are known from Central America.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Fish Creek Mts, *von Wedel 2369* (MO, US). PANAMA: Cerro Jefe, *Dwyer et al. 7246* (MO).

5. STRYCHNOS

Strychnos L., Sp. Pl. 189, 1753; Gen. Pl. ed. 5, 86, 1754.

Lianas or scandent shrubs, sometimes of considerable length, typically with coiled tendrils, sometimes also with spines, the branches opposite. *Leaves* opposite, sessile or petiolate, the petioles connected by stipular lines (well-developed stipules usually not present); blades of various shapes, simple, entire, typically 3-5-plinerved, coriaceous or membranous. *Inflorescences* terminal or axillary or both, basically cymose. *Flowers* ☿, 5-merous or less frequently 4-merous, the pedicels 0-5 mm long; calyx-lobes exceeding the calyx-tube or sometimes equal to it, often imbricate basally, broadly ovate to linear; corolla yellow to pale green or white, salverform to virtually rotate, often carnosulous, the tube 0.1-2.5 cm long, the lobes valvate in bud, shorter than or equal to or longer than the corolla-tube, glabrous to very conspicuously pubescent internally; anthers included or exserted, glabrous or pilose, the filaments usually attached to the corolla-tube throughout most of their length; ovary subglobose or ovoid, 2-locular or sometimes 1-locular or incompletely 2-locular, the style unbranched, the stigma small, capitate, slightly 2-lobed. *Fruit* a berry, ovoid or globose, 1-9 cm in diameter, the shell very hard to somewhat fleshy, the pulp soft; seeds one to many, 0.5-2.5 cm long.

A tropical and subtropical genus of about 235 species. Representatives occur on every continent but Europe, the greatest percentage of species probably occurring in Africa. Approximately 64 species are known in the New World; five (six?) species occur in Panama.

Various species of *Strychnos* are the source of a large number of physiologically active alkaloids. Seeds of the Asiatic *S. nux-vomica* L. and *S. ignatii* Bergius are

Fig. 4. *Potalia amara* Aublet: A, habit (×¼); B, flower (×3½); C, section of flower showing pistil and two of the stamens (×4); D, fruit (×1); E, seed (×4). A-C after *von Wedel 2369* (MO); D-E after *Dodge et al. 6067* (MO), Costa Rica.

notable as a source of strychnine and brucine. The bark of a number of American species, including *S. toxifera, S. peckii* and *S. panurensis,* is used by South American Indians as a main or secondary ingredient of the paralysing Curare arrow poison. Of the three American species mentioned, probably only *S. toxifera* provides a main ingredient.

Useful references:

Krukoff, B. A. & J. Monachino, The American species of *Strychnos.* Brittonia **4:** 248-322, 1942.

Krukoff, B. A., Supplementary notes on the American species of *Strychnos.* Mem. N. Y. Bot. Gard. **12**(2): 1-94, 1965.

a. Inflorescences terminal.
  b. Corolla-tube not exceeding the calyx in length; style equal to or shorter than the ovary; puberulence of the branchlets usually not exceeding 0.1 mm in length .....5. *S. nigricans*
  bb. Corolla-tube much longer than the calyx; style at least 3 times the length of the ovary; puberulence of the branchlets considerably exceeding 0.1 mm in length (though sometimes sparse).
    c. Corolla externally conspicuously hirsute with rufescent trichomes 0.5-3.5 mm long; anthers inserted at the throat of the corolla-tube or with the tips protruding; branchlets conspicuously hirsute with rufescent trichomes 0.5-3.5 mm long; leaf-blades universally pubescent (though sometimes sparsely so) .....2. *S. toxifera*
    cc. Corolla externally papillose but glabrous; anthers conspicuously exserted; branchlets rather sparsely pilose with trichomes 0.2-1 mm long; the very sparse pubescence of the leaf-blades confined mainly to the principal veins and the margin .....1. *S. panamensis*

aa. Inflorescences axillary.
  d. Corolla-tube equal to or somewhat shorter than the corolla-lobes; flowers 5-merous; free-portion of filaments 1 mm or more in length and the anthers manifestly exserted; fruit with 1 or 2 seeds .....4. *S. panurensis*
  dd. Corolla-tube obviously longer than the corolla-lobes (if approximately equal then the flowers 4-merous); free-portion of filaments obsolete or essentially so (less than 0.5 mm long) and the anthers inserted at the throat of the corolla-tube (sometimes with the tips protruding); fruit with numerous seeds.
    e. Flowers 5-merous; corolla externally conspicuously short-pubescent with trichomes 0.1-0.4 mm long, the lobes internally densely lanate toward the base and at least sparsely lanate above the middle; calyx-lobes broadly ovate-deltoid; leaf-blades with the inner pair of principal nerves glabrous in the axils .....6. *S. peckii*
    ee. Flowers 4-merous; corolla papillose but glabrous externally, the lobes internally bearded at the base but otherwise glabrous; calyx-lobes lanceolate or ovate-lanceolate; leaf-blades frequently barbate in the axils of the inner pair of principal nerves .....3. *S. dariensis*

1. **Strychnos panamensis** Seemann, Bot. Voy. Herald 166, 1854.—Fig. 5 (A-D).

Vine or clambering shrub; young branchlets green, compressed, sparsely or moderately (but unevenly) pilose in strips down opposite sides with slender and unbranched trichomes 0.2-1 mm long; older branches terete, glabrous, developing brown or grayish-brown bark. *Leaves* with petioles 1.5-7(-15) mm long which are pilose (but not densely so) with trichomes to 1 mm long; blades ovate to ovate-lanceolate or elliptic, apically acuminate or sometimes acute, basally acute to

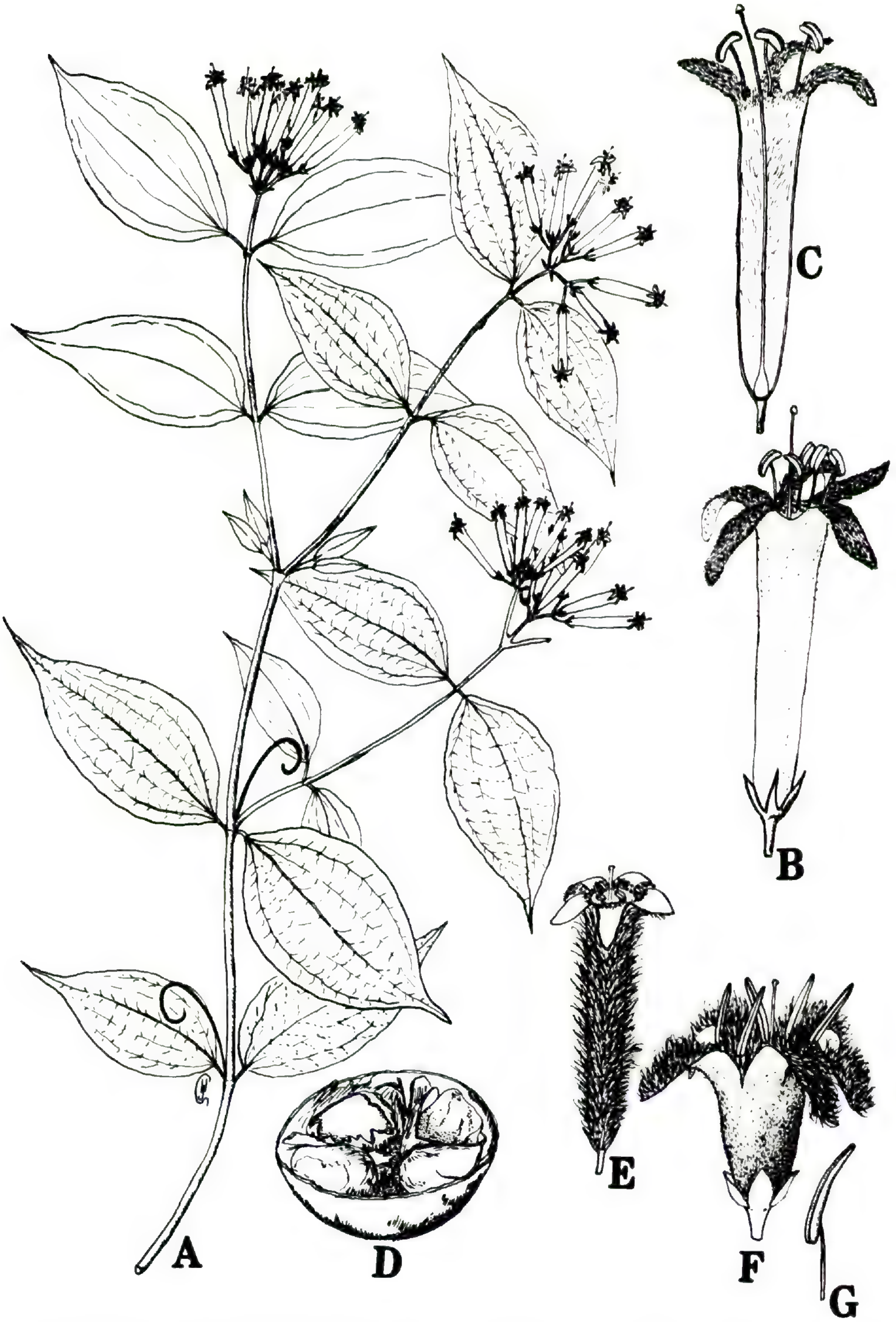

Fig. 5. *Strychnos panamensis* Seemann: A, habit (×½); B, flower (×2); C, section of flower showing pistil (×2); D, section of fruit showing seeds (×½). A-C after *Hayden 17* (MO); D after *Tyson & Blum 3570* (MO). *S. toxifera* Rob. Schomb.: E, flower (×2½). After *Pittier 2666* (US). *S. panurensis* Sprague & Sandwith: F, flower (×5); G, stamen (×7). After *Klug 4082* (MO), Peru.

rounded or cordate, 4-12 cm long, 1.5-5 cm broad, membranous to subcoriaceous, very sparsely pilose along the principal veins (above and below) and along the margins with simple trichomes 0.2-1 mm long, less frequently entirely glabrous, 3(5)-plinerved, the primary nerves raised below and somewhat impressed above, the reticulation on both surfaces ranging from apparent to prominulous (rarely obscure above). *Inflorescences* terminal, cymose. *Flowers* with pedicels obsolete to ca 3.5 mm long (in each 3-flowered dichasial component of the terminal cyme the central pedicel is manifestly shorter than the 2 lateral pedicels, the central flower thus often appearing subsessile); calyx-lobes slender-lanceolate to slightly ovate-lanceolate, 2.5-4 mm long, marginally ciliate but otherwise glabrous, the tube absent to ca 0.5 mm long; corolla salverform, white to green or yellow, externally minutely papillose (not with well defined trichomes), the tube 13-24 mm long, 1-2.5 mm broad, conspicuously pilose internally with trichomes to 1 mm long except near the throat and base, the lobes linear-lanceolate, 3-4.5 mm long, densely papillose internally; anthers 0.7-1 mm long, glabrous, exserted from the corolla-tube by 1.5-3 mm on filaments adnate to the corolla-tube to the throat but extending beyond; ovary 1-1.5 mm long, 2-locular, passing almost imperceptibly into the long tapering style, the style exserted by 2-4 mm, terminated by a small capitate and unlobed stigma. *Fruit* globose, 2.5-8 cm in diameter, frequently turning orange, the pulp yellowish or light orange, several to ∞-seeded.

Occurring from the Pacific Coast of tropical Mexico, through Central America to northeastern Venezuela and northern Colombia. Krukoff (loc. cit. 30) states that *S. panamensis* is "By far the most frequently collected species in Central America and one of the three species (the other two being *S. tabascana* and *S. nigricans*) which are found in Mexico."

CANAL ZONE: vic of Summit, *Allen 4573* (F); Barro Colorado I, *Bailey & Bailey 306* (F), *Bangham 431* (F, US), *Dwyer 1475* (MO), *Frost 185* (F), *Killip 39995* (US), *40007* (US), *Shattuck 310* (F), *Standley 31307* (US), *Wetmore & Abbe 138* (F), *Zetek 3617* (F, MO); nr beach at Fort Kobbe, *Duke 4220* (MO); shore, Fairchild Point, *Hayden 17* (MO); Río Agua Salud, nr Frijoles, *Piper 5865* (US), *5875* (US); along the Trinidad River, *Pittier 4007* (US); Balboa, *Standley 25457* (US); hills W of the Canal, nr Gatun, *Standley 27213* (US); Río Paraíso, above East Paraíso, *Standley 29868* (US); vic of Fort Sherman, *Standley 30978* (US); Obispo, *Standley 31710* (US); vic of Río Cocoli, rd K-9, on roadside, *Stern et al. 35* (MO); Chiva Chiva Trail nr Miraflores Lake, *Tyson & Blum 3570* (MO); Río Cocoli opposite lighthouse, *White 100* (F, MO); mouth of Cocoli River, *White 144* (F, MO); vic of Miraflores Lake, *White 168* (F, MO). CHIRIQUÍ: vic of Puerto Armuelles, *Woodson & Schery 815* (MO, US). COCLÉ: Penonomé & vic, *Williams 389* (US). DARIEN: betw Quebrada Venado & Peje Swamp on the headwaters of Río Tuqueza, *Bristan 1029* (MO); Río Chucunaque, betw Río Membrillo & Río Subcuti, *Duke 8604* (MO); Río Pucro, below village of Pucro, *Duke 13139* (MO); Puerta St. Dorothea, *Dwyer 2208* (MO, US). PANAMA: La Campana, *Bouché 12* (US); Vacamonte Bay, *Bouché s.n.* (MO); gallery along Río Terable, nr Pan-Amer. Hwy & El Llano, *Duke 5672* (MO); San José I, mouth of Río Marino, *Johnston 1299* (MO, US); Taboga I, *Maxon 6910* (US), *Pittier 3543* (US), *Seemann s.n.* (type K, not seen), *Standley 27047* (US), *27848* (US), *Woodson et al. 1517* (F, MO); Río Tapia, *Standley 26125* (US), *28086* (US); nr the big swamp E of the Río Tocumen, *Standley 26596* (US); Río Tocumen, *Standley 26730* (US), *29446* (US); Juan Díaz, *Standley 30564* (US); betw Matías Hernández & Juan Díaz, *Standley 32091* (US).

2. **Strychnos toxifera** Schomb. ex Bentham in Hooker, Jour. Bot. **3:** 240, 1841.—Fig. 5(E).

Vine, woody; branchlets hirsute with slender, unbranched, mostly straight, rufescent trichomes 0.5-3.5 mm long; older branches eventually glabrous, thickening, developing gray or grayish-brown bark. *Leaves* spreading; petioles 1-6 mm long, typically conspicuously fulvous-hirsute, sometimes twisted or curved; blades ovate or lanceolate to elliptic or oblanceolate, 4.5-20 cm long, 2-8 cm broad, apically acuminate, basally rounded or subcordate to acute, chartaceous or sometimes membranous, sparsely to moderately pubescent above and below with trichomes similar to those of the branchlets (often rather densely hirsute below on the midvein toward the base), (3)5-plinerved, the primary nerves raised below and impressed above, the reticulation prominulous to faint on both surfaces. *Inflorescences* terminal, cymose. *Flowers* with pedicels obsolete to 5.5 mm long (the median pedicel of each dichasial unit much shorter than the laterals); calyx-lobes lanceolate to subulate, 1-7 mm long, hirsute but usually not densely so, the tube absent or virtually so; corolla salverform, white or yellow, externally conspicuously hirsute with simple, straight or interwoven, rufescent trichomes 0.5-3.5 mm long, the tube 10-16 mm long, 1-1.5 mm broad, pilose internally on the upper ½ with trichomes to ca 1.5 mm long, the lobes internally minutely papillose throughout, in addition densely bearded at the base, 1.5-2.5 mm long, lanceolate to oblong-lanceolate or ovate-lanceolate; anthers 0.7-1 mm long, ovate, glabrous, inserted at the corolla-throat (often with the tips protruding), the free-portion of the filaments obsolete or essentially so; ovary 2-locular, subglobose, ca 1 mm long, with the carpellary sutures evident externally, passing manifestly into the long and tapering style, the style, glabrous, exserted by 0.5-2 mm, terminating in a small capitate stigma. *Fruit* hard, bluish-green, 4-7 cm in diam.

Costa Rica to Brazil, Ecuador and French Guiana. According to Krukoff (loc. cit. 34), *S. toxifera* is "common in the Canal Zone."

CANAL ZONE: Barro Colorado I, *Kenoyer 479* (US), *624* (US), *Standley 31311* (US), *41042* (US), *Wetmore & Abbe 98* (F); hills around the Agua Clara Reservoir, nr Gatun, *Pittier 2666* (US); hills N of Frijoles, *Standley 27542* (US); Gamboa, *Standley 28386* (US); France Field, *Stevens 196* (US). SAN BLAS: along headwaters of Río Mulatupo, *Elias 1747* (MO).

3. **Strychnos darienensis** Seemann, Bot. Voy. Herald 166, 1854.

Liana; branchlets green, compressed, obscurely puberulent with trichomes 0.3 mm long or less to glabrous, the older branches glabrous. *Leaves* with petioles 1-7 mm long which are glabrous or obscurely puberulent; blades ovate or lanceolate to elliptic or oblanceolate, 5-19 cm long, 2.5-9.5 cm broad, apically acuminate, basally rounded or subcordate to acute, chartaceous or subcoriaceous, often drying olive-ocher yellow, glabrous or essentially so at maturity (sometimes sparsely and minutely puberulent along the primary nerves and/or with a few basal-marginal cilia), 3(5)-plinerved, the primary nerves raised below, impressed above, the inner pair of principal nerves typically barbate in the axils with rufescent trichomes to ca 0.8 mm long, the reticulation faint to prominulous on both sur-

faces. *Inflorescences* axillary, condensed-thyrsoid or short-racemose. *Flowers* with pedicels to ca 2 mm long; calyx-lobes lanceolate or ovate-lanceolate, 1-1.5 mm long, apically acute to acuminate, externally hirsutulous with short rusty tichomes or essentially glabrous, marginally ciliate, the tube lacking to ca 0.5 mm long; corolla minutely papillose externally (not with definite trichomes), the tube pilose within, the lobes internally bearded at the base but otherwise glabrous; anthers subsessile; style glabrous. *Fruit* glabrous, ca 4 cm in diam, yellow; seeds numerous, irregularly oblong, ca 20 mm long and 15 mm broad, 4 mm thick.

Costa Rica and Panama to Brazil, Peru and Bolivia.

CANAL ZONE: Barro Colorado I, *Carpenter 60* (F), *Standley 41005* (US), *Woodworth & Vestal 612* (F). COLÓN: betw France Field, Canal Zone & Cativa1, *Standley 30174* (US). VERAGUAS: Coyaba I [Isla de Coiba] & coast of Darien, *Seemann 632* (type K, not seen).

4. **Strychnos panurensis** Sprague & Sandwith, Kew Bull. **1927:** 132, 1927.—Fig. 5(F-G).

Shrub or woody vine; branchlets distally hirsutulous with ascending or upwardly curving trichomes to ca 0.2 mm long, less frequently glabrate, the older branches glabrous, terete or subtetragonal. *Leaves* with petioles 3-10 mm long; blades ovate or ovate-lanceolate to elliptic-lanceolate or elliptic-obovate, apically acuminate or subacuminate, basally cuneate to rounded, 4-20 cm long, 2-7.5 cm broad, essentially glabrous (occasionally sparsely and minutely puberulent below on the primary nerves and above toward the base of the medvein), grayish-green and sublustrous on drying, 3(5)-plinerved, the primary nerves conspicuously raised below, the reticulation intricate and prominulous to prominent on both surfaces. *Inflorescences* axillary, thyrsoid, rather elongate, the main axis bearing several pairs of opposite floriferous branchlets. *Flowers* with pedicels virtually obsolete to 4.5 mm long and hirsutulous to essentially glabrous; calyx-lobes ovate to deltoid- or rhombic-ovate, apically acute or subacuminate, to 1.5 mm long, externally glabrous to papillose or minutely hirsutulous, marginally rather conspicuously ciliate; corolla white, saverform, externally papillose but otherwise glabrous, the tube 1.5-4 mm long, internally pilose, the lobes 2-5.5 mm long, linear-lanceolate, often recurved, lanate on the whole inner surface; anthers 1.5-2 mm long, glabrous, linear or narrowly trullate, basally rounded, exserted by 1.5-4.5 mm, the filaments becoming free at the throat of the corolla; ovary subglobose, ca 1 mm long, passing manifestly into the style, the style glabrous, exserted by 2-5 mm from the corolla-throat, the stigma small and barely aparent (only slightly enlarged), single or 2-parted. Fruit ovoid to subglobose, ca 2 cm long, 1.5-2 cm broad, yellowish-green, with 1 or 2 large black seeds.

Panama to Peru and Brazil.

PANAMA: halfway betw Goofy Lake & Cerro Jefe, *Blum et al. 2271* (MO); Cerro Jefe, *Dwyer 7092* (MO), *7287* (MO), *Tyson et al. 4399* (MO).

Strychnos panurensis was previously unreported from Panama, being known only from South America.

5. **Strychnos nigricans** Progel in Martius, Fl. Bras. **6**(1): 280, 1868.

S. brachistantha Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **12**: 412, 1936.

Shrub, erect or scandent, sometimes climbing; branchlets usually puberulent with minute (to 0.1 mm long), erect, grayish trichomes which are sometimes mamilliform; older branches glabrous, developing dark grayish-brown bark, the lenticels often conspicuous and orbicular to ellipsoidal or oblong. *Leaves* with petioles 1-7 mm long which are minutely puberulent to essentially glabrous; blades ovate or lanceolate to elliptic or obovate, apicaly acuminate (sometimes long-acuminate), basally rounded or subcordate to cuneate, 2.5-14 cm long, 1-4 cm broad, entirely glabrous on both surfaces or puberulent below on the primary nerves with trichomes to 0.1 mm long, frequently barbate in the axils of the inner pair of principal nerves with trichomes to ca 0.6 mm long, 3(5)-plinerved (occasionally showing a tendency toward pinnate nervation), the primary nerves raised below, impressed above, the reticulation obscure or faint above, faint to prominulous below. *Inflorescences* terminal, cymose, sometimes paniculoid, the various branches essentially glabrous or minutely grayish-puberulent with trichomes to 0.1 mm long. *Flowers* with pedicels obsolete to 2.5 mm long (the central pedicel of a dichasial unit often reduced); calyx-lobes ovate to ovate-lanceolate, entirely glabrous or else marginally ciliate, up to 1.2 mm long, often unequal and patulous, exceeding the slight calyx-tube; corolla externally glabrous, the tube 1 mm or less in length, internally glabrous, the lobes ovate or ovate-lanceolate, 1-1.5 mm long, internally papillose on the upper portion, bearded internally at the middle or more toward the base; anthers 0.7-1 mm long, glabrous, sessile or subsessile at the throat of the corolla-tube; ovary subglobose to ovoid, ca 1 mm long, the style glabrous, 1 mm long or less, the stigma small, capitate. *Seeds* with a white, wooly covering.

Mexico (Jalisco, Vera Cruz and Tabasco), Central America and Brazil.

CANAL ZONE: hills N of Frijoles, *Standley 27418* (US).

6. *Strychnos peckii* B. L. Robinson, Proc. Amer. Acad. **49**: 504, 1913.

No specimen of *S. peckii* has been collected in Panama. However, this species has been collected widely in Central America (Guatemala, British Honduras and Costa Rica). In South America *S. peckii* is known from Colombia, Venezuela, the Guianas, Ecuador, Brazil and Bolivia. The apparent gaps in distribution will probably disappear as collecting continues. Krukoff (loc. cit. 47) states that "it doubtless occurs in Honduras, Nicaragua and Panama."

6. POLYPREMUM

Polypremum L., Sp. Pl. 111, 1753; Gen. Pl. ed. 5, 50, 1754.

Polypremum procumbens L. is the only species of this genus. No collection from Panama is known to me. However, the species is widespread (southeastern United States to northern South America and the West Indies) and its apparent absence from Panama may be due to insufficient collecting and to its inconspicuous nature in the field.

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Numbers in **boldface** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 166. HYDROPHYLLACEAE[1]

BY THOMAS B. CROAT
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Herbs, annual, biennial or perennial, rarely subshrubs, frequently pubescent, sometimes also spiny or glandular. *Leaves* alternate or radical, rarely opposite, estipulate; blades entire to pinnately (rarely palmately) lobed. *Inflorescences* mostly scorpioid cymes or flowers solitary, rarely corymbose. *Flowers* ☿, actinomorphic, generally 5-merous with reduction to 2 in the pistil; sepals distinct or connate at the base, often accrescent in fruit; corolla sympetalous, rotate, campanulate or funnelform, the 5 lobes imbricate or rarely contorted; stamens epipetalous and alternate with the corolla-lobes, included or exserted, the anthers versatile, oblong, ovoid or sagittate, 2-thecate with introrse, longitudinal dehiscence; pollen grains 3-colporoidate, the sexine reticulate; disc hypogynous or absent; pistil solitary, the ovary superior, 1- or more rarely 2-locular, the ovules 2-∞, sessile or pendulous, anatropous or amphitropus, the styles usually 1 (± divided) or 2, rarely 3-5, the stigma generally capitate. *Fruit* a loculicidal or septicidal capsule; seeds with a fleshly or cartilaginous endosperm, the embryo small and straight.

A family of 18-19 genera which is chiefly Andean and North American (16 genera confined to the latter), but occurs on all continents except Europe and Australia; two genera presently reported from Panama.

a. Stems with spines 10-25 mm long, no setae; leaves 3-12 cm long .....1. *Hydrolea*
aa. Stems without spines, setae if present less than 8 mm long; leaves frequently up to 47 cm long (largest leaves always more than 15 cm long) .....2. *Wigandia*

1. HYDROLEA

Hydrolea L., Sp. Pl. ed. 2, 328, 1762.

Herbs, annual or perennial, or shrubby plants with capitate glandular hairs or glabrous, spiny (in Panama). *Leaves* alternate, entire. *Inflorescences* corymbose or flowers in axillary or terminal cymes. *Florets* rarely sparse or in cincinni; calyx parted nearly to the base, sometimes accrescent; corolla blue or rarely white, campanulate-rotate, deeply parted; stamens glabrous, the filaments dilated at the base, inserted in the tube of the corolla, the anthers sagittate, dorsifixed; ovules numerous

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[1] Assisted by National Science Foundation Grant No. GB-5674 (Principal Investigator, Walter H. Lewis).

(up to 400), the styles distinct, 2, rarely 3-5, the stigmas capitate-clavate. *Capsule* ovoid or globose, loculicidal, septicidal or irregularly dehiscent; seeds small, longitudinally rugose-striate, the embryo 0.4-0.5 mm long.

A genus of nearly world-wide distribution having ca 20 species in tropical regions extending into temperate areas especially in eastern North America; monographed by Brand [in Engler, Pflanzenreich **59**(IV, 251): 174-186, 1913]; one variable species presently known from Panama.

1. **Hydrolea spinosa** L., Sp. Pl. ed. 2, 328, 1762.—Fig. 1.

Nama spinosa (L.) O. Kuntze, Rev. Gen. **2**: 434, 1891.

Spiny, stout, erect (sometimes shrub-like) *herb*, sparsely to densely pilose or glandular-pilose throughout; stem branched, 6-13 dm tall with few to many spines 1-2.5 cm long. *Leaves* sessile or short-petiolate, elliptic to oblong or lanceolate, rarely obovate, highly variable in size and shape; cauline leaves 3-12 cm long, 5-30 mm wide, the apex acute, the base cuneate to attenuate, entire. *Flowers* fragrant, shortly pedunculate, congested corymbosely at the apex or frequently sparse and solitary on short branches along the main stem or branches; sepals 5, oblong to broadly lanceolate, acute, conspicuously veined, 5-9 mm long, glandular-pilose; corolla bright blue to purple, 10-15 mm in diam, divided to near the middle, the 5 lobes imbricate; stamens 5, included or exserted; pollen grains subprolate-prolate (28 × 21μ); ovary oblong-ovoid, bilocular with axile placentation, pubescent or glandular-pubescent, together with the styles less than 12 mm long at anthesis (frequently much more after fruit has expended), the styles 2-3-(4-5), frequently glandular at the base, usually longer than the calyx at anthesis, rarely shorter than the calyx. *Capsule* rounded, thin-walled, regularly or irregularly dehiscent; seeds small, numerous.

From Mexico throughout Central America and the West Indies to Colombia and Ecuador on the Pacific Coast and on the Atlantic to southern Brazil and Uruguay; moist areas; known in Central America as *spina de vagre* (fide Brand).

Our plants are all of the var. *spinosa*.

BOCAS DEL TORO: Changuinola valley, Pontoon Bridge, *Dunlap 318* (F). CANAL ZONE: Chagres, *Fendler 236* (MO); s. loc., *Grisebach s.n.* (MO). HERRERA: vic of Ocú, ½ mi NE, open pasture, *Stern et al. 1707* (MO). PANAMA: nr Chepo, savannas, *Hunter & Steyermark s.n.* (MO).

2. WIGANDIA

Wigandia H.B.K., Nov. Gen. Sp. Pl. **3**: 127, 1818.

Herbs, large somewhat woody at the base to tree-like, up to 3 m tall, frequently with stinging hairs. *Leaves* very large, subentire. *Flowers* in regularly arranged cincinni; calyx usually divided to the base; corolla large, purplish, infundibuliform-campanulate or shortly hypocrateriform; stamens somewhat exserted, partly adnate with the corolla-tube, the filament barbed for the most part; styles 2, elongate, the stigma capitate-clavate. *Capsule* loculicidally and septicidally dehiscent; seeds small, brown, winged, the embryo barely conspicuous.

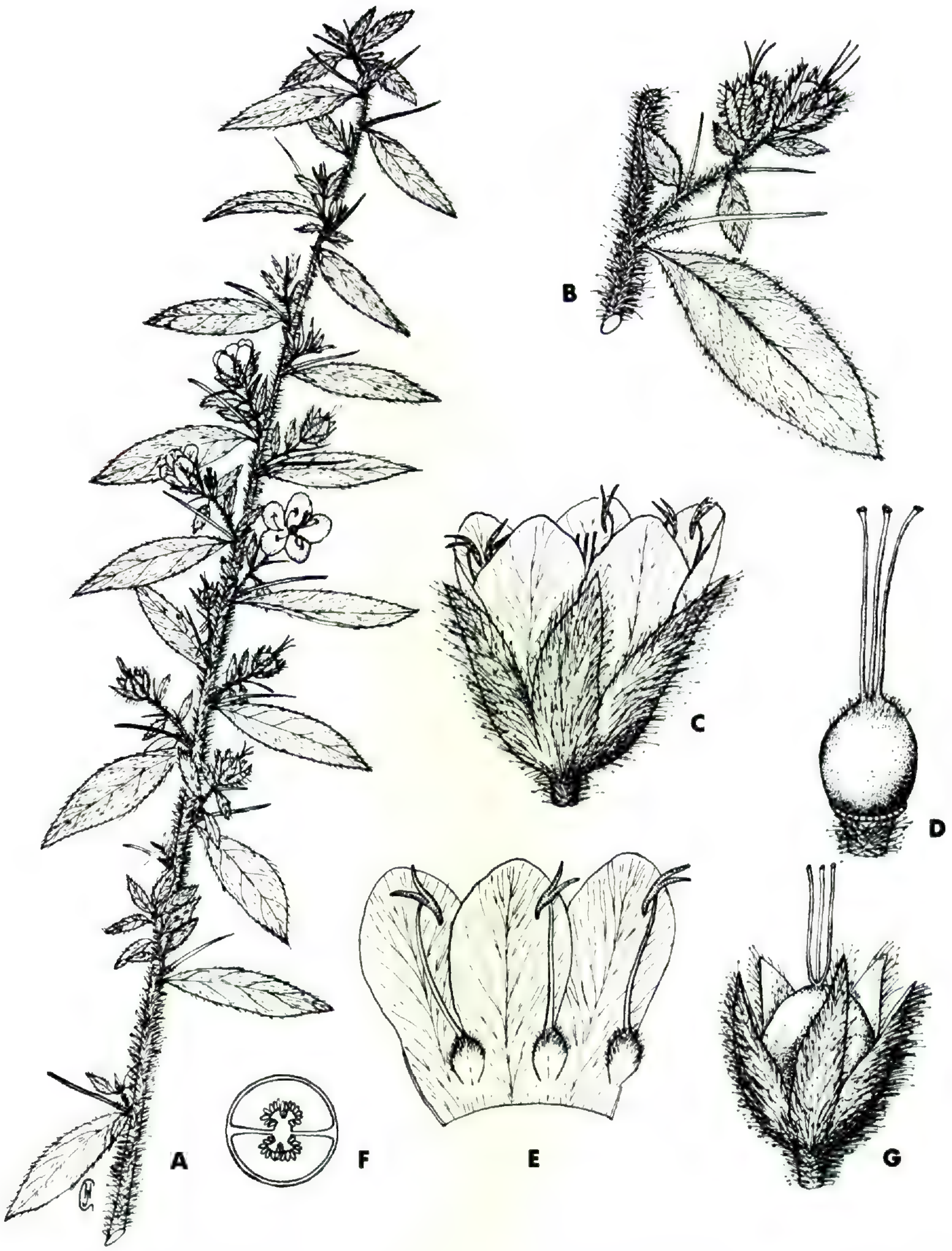

Fig. 1. *Hydrolea spinosa* L.: A, habit (×½); B, branch of inflorescence (ca ×1) C, flower (ca ×3); D, ovary (ca ×4); E, section of corolla (ca ×3); F, ovary cross-section (ca ×6); G, fruit (ca ×3). After *Allen & Hunter 40* (MO).

A tropical genus of 5-6 species restricted to Central and South America; [cf. Brand in Engler, Pflanzenreich **59**(IV, 251): 134-137, 1913]. Only *W. caracasana* is reported for Panama.

1. **Wigandia caracasana** H.B.K., Nov. Gen. Sp. Pl. **3:** 100, 1818.

Erect, robust, suffrutescent *herb* (sometimes appearing shrublike) seldom more than 3 m tall, usually entirely pubescent with stiff or soft whitish hairs except for outer rim and inside of corolla and upper portion of the styles, the pubescence conspicuous and variable, the hairs often coarse and stinging, often with glandular hairs interspersed with small viscid globules. *Leaves* alternate, long-petiolate (up to 10 cm); blades up to 50 cm long and 37 cm wide, broadly ovate to oblong-elliptical to almost rounded, obtuse, subcordate at the base, coarsely and irregularly double-crenate to double-serrate, sparsely to densely hispid above (rarely sericeous or subglabrous), densely white-tomentose to almost wooly below. *Flowers* in an elongate cincinnus regularly arranged in a terminal thyrse or panicle and bearing pubescence similar to the stem and inflorescence (usually densely hispid to sericeous); sepals 5, 8-15 mm long, lanceolate; corolla violet to blue, turning medium reddish-brown on drying, up to 3 cm broad, 5-lobed, the lobes equal to the tube in length; stamens 5, pubescent, usually included; ovary with style 13-17 mm long, the styles 2, clavate-capitate, usually longer than the ovary. *Capsule* dark brown, oblong to ovoid, equal to or longer than the calyx, longitudinally dehiscent, the valves 2 persistent; seeds ∞.

Southern Mexico to Colombia and Venezuela; hedges, thickets and roadsides mostly 1,100-1,600 m; known in Central America as *ortiga* (fide Brand) or *ortiga de montana* (fide Standley, in Costa Rica).

Wigandia caracasana is quite variable in Panama and plants are found which are densely long-pubescent and lack setae while others are less densely pubescent but have stiff setae. In other cases plants are densely short-pubescent and lack setae. Gibson (Fieldiana: Bot., in press) concludes that many of the taxa as treated by Brand (loc. cit.) for Central America should be included under *W. urens* (Ruiz & Pavon) H.B.K.

For an ilustration of the setaceous form of this species see Constance (Brittonia **15:** 280, *fig. 1*, 1963).

CHIRIQUÍ: upper valley of Río Chiriquí Viejo, alt 4500-6000 ft, *Allen 1498* (MO); Boquete District, Volcán de Chiriquí, open areas, alt 8500 ft, *Davidson 972* (F, MO); town of Volcán, ca 4600 ft, *Duke 9151* (MO); valley of upper Río Chiriquí Viejo, *White 317* (MO). LOS SANTOS: 12 mi S of Macaracas, *Tyson et al. 3064* (MO).

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